DISTURBANCE, SUCCESSION, AND THE COEXISTENCE OF SPECIES IN A LOWLAND PODOCARP FOREST, SOUTH WESTLAND, NEW ZEALAND.

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He iti hoki te mokoroa, nāna i kakati te kahikatea

The huhu grub was small, but it chewed through the kahikatea

Maori proverb

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ABSTRACT

Vegetation change in six forest stands affected by flood and wind disturbance was investigated using stand history reconstruction in a lowland podocarp forest, south Westland, New Zealand. A method is described for identifying even-aged patches of trees from tree location and age data. Identification of even-aged patches of trees, along with size and age structures, and stem spatial distributions, were used to reconstruct the spatial and temporal patterns of tree establishment in response to past disturbance.

Periodic, major disturbance had affected the composition and structure of all six stands. In four of the stands floods formed extensive, continuous canopy openings and initiated regeneration of relatively even-aged patches of trees. In the remaining two stands windthrow of canopy trees occurred over an extended period and resulted in abundant but patchy regeneration in smaller treefall openings.

Species differed in their patterns of regeneration in response to disturbances of different type and intensity. Establishment site preferences and stem spatial distributions showed that the four species studied partitioned establishment sites along gradients related to canopy cover and forest floor microrelief. Partitioning of establishment sites may contribute to the maintenance of species diversity in these forests. Moreover, disturbance is critical for continued coexistence as it is the source of much of the environmental variation to which species differentially responded.

The composition and structure of regenerating patches was determined by the interaction between species regeneration requirements and the availability of suitable establishment sites. The type and intensity of disturbance and underlying environmental gradients influenced the availability of establishment sites within canopy gaps and hence subsequent forest establishment.

Catastrophic floods formed extensive openings and left relatively homogeneous deposits of silt. Regeneration on these sites was dominated by *Dacrycarpus dacrydioides*. Less intense flooding left logs and stumps that provided sites for establishment of *Dacrydium cupressinum*, *Prumnopitys ferruginea*, and *Weinmannia racemosa*. On older surfaces drainage patterns influenced establishment in openings formed by treefalls. Regeneration on drier sites was dominated by *D. cupressinum*, *P. ferruginea*, and *W. racemosa* reflecting the predominance of better drained level and elevated microsites. In contrast *D. dacrydioides* dominated regeneration on poorer drained surfaces that had abundant wet depressions.

The importance of disturbance in influencing forest composition and patterns of species turnover suggests that a non-equilibrium model of vegetation change is appropriate for understanding the dynamics of these forests.

CHAPTER I

INTRODUCTION

A central idea in plant ecology concerns the maintenance of species diversity (Glitzenstein *et al.* 1986). How do two or more species with similar requirements coexist in the face of tendencies towards competitive exclusion? (eg., Grubb 1977; Connell 1978; Shmida & Ellner 1984). One explanation is that species can coexist in a constant environment if each specialises in a particular region of the resource spectrum. That is, each species occupies a different niche.

This explanation assumes that the plant community has reached a competitive equilibrium and is not undergoing compositional change due to competition (Connell 1978; Pickett 1980). However, recent reviews suggest that plant communities rarely if ever reach competitive equilibrium (Drury & Nisbet 1971; Pickett 1980). Rather, natural disturbances, such as fires and windstorms, repeatedly disrupt the process of competitive assortment and so prevent the attainment of competitive equilibrium (Pickett 1980; see for example Wright & Heinselman 1973; White 1979).

Recent conceptual models of forest dynamics include disturbance as an integral component of the forest system (eg., Drury & Nisbet 1971; Veblen *et al.* 1980; Pickett *et al.* 1987). Disturbances form openings (gaps) in the forest canopy, altering the availability of resources for plant growth and allowing new individuals to establish or grow (Canham & Marks 1985). Infilling of small gaps occurs through lateral growth of surrounding vegetation but larger gaps are filled through growth into the canopy of new individuals (Runkle 1985), forming a patch. The disturbance regime, which determines the spatial and temporal patterns of patch creation, along with the process of gap infilling and subsequent changes in patch cohort structure and composition, has been termed patch dynamics

(Pickett & Thompson 1978). Many forested landscapes consist of a mosaic of patches of different size and structure, and at different stages of development following gap formation (Jones 1945; Oliver 1981; Whitmore 1982). The concept of patch dynamics provides a framework for understanding the patterns and processes occurring in many plant communities (see papers in Pickett & White 1985).

Recognition of the importance of natural disturbance and the non-equilibrium state of many forest systems has led to a reformulation of ideas about species coexistence and species turnover at a site (succession) (Drury & Nisbet 1973; Connell & Slayter 1977; Pickett 1980; Pickett *et al.* 1987; Burrows 1990). For example, a number of authors have argued that natural disturbances increase the possibility of multi-species coexistence by introducing heterogeneity into forest systems, thereby increasing the opportunities for habitat partitioning (Grubb 1977; Denslow 1980, 1985; Orians 1982).

Disturbances vary in their effect on different sites. Disturbances of different type and intensity form openings of differing size, structure and internal heterogeneity that have contrasting gap micro-environments (Bazzaz 1983). Certain life-history traits may give a species a competitive advantage in the set of environmental conditions associated with gaps of a particular size and structure. For example, fast growing, light-demanding tree species are generally adapted for success in large gaps where light levels are high. In contrast, slower growing species that can tolerate low light levels are adapted for success in small gaps (Bazzaz & Pickett 1980; Whitmore 1982).

In many forested landscapes the diversity of micro-environments found in different disturbance openings may contribute to the maintenance of species diversity (Denslow 1985). Furthermore, because the size of canopy gaps correlates with important environmental parameters such as light level (eg., Barton *et al.* 1989), gap size is viewed as a principle axis of differentiation among species (Denslow 1980).

Closely linked to the idea of species coexistence is species turnover at a site, or succession. Patch dynamics provides a framework for understanding the mechanisms of forest succession (Pickett *et al.* 1987; Pickett & McDonnel 1989). Change in forest canopy composition occurs when a different species occupies an opening formed by the death of a canopy tree. This change in canopy composition can occur for two reasons (Pickett *et al.* 1987). First, the newly colonising species has an advantage over others in availability at the site (eg., the colonising species was present as advance regeneration or rapidly occupied the site). Second, the newly colonising species has a competitive advantage in survival and performance in the set of environmental conditions encountered in the opening.

Forest succession is therefore a consequence of species availability and variation in gap environments through time, influenced by both physical and biotic factors. Patterns of succession are determined by the interaction between gap environments, the differential availability of species, and the differential performance of species in the sets of environmental conditions encountered (Drury & Nisbet 1973; Pickett 1976; Pickett *et al.* 1987).

Disturbances are important in structuring many forest communities (White 1979; White & Pickett 1985) including those in New Zealand (Veblen & Stewart 1982). Flood and wind disturbance have a major impact on the structure and composition of dense podocarp forest, on post-glacial outwash surfaces in south Westland, New Zealand (Hutchinson 1928, 1932; Foweraker 1929; Poole 1937; Wardle 1974; Six Dijkstra *et al.* 1985). While a number of studies have recognised the importance of natural disturbance in these forests few have quantitatively examined the effect of disturbance on forest patterns and processes. No studies have examined how disturbances of different type and intensity affect forest structure, composition, and patterns of succession.

The aim of the present study is to examine patterns of regeneration in openings formed by disturbances of different type and intensity in lowland podocarp forest, south Westland, New Zealand. Vegetation change in six forest stands affected by flood and wind disturbance is investigated using stand history reconstruction (eg., Henry & Swan 1974; Oliver & Stephens 1977; Lorimer 1985). Age and size structures, and stem spatial locations are used to identify even-aged patches of trees and to reconstruct the spatial and temporal patterns of tree establishment in response to past disturbance.

Species establishment site preferences and stem spatial distributions show that species partitioned establishment sites along gradients related to canopy cover and forest floor microrelief. The distribution of species within patches and differences in composition among patches was related to the distribution and availability of suitable establishment sites. The type and intensity of disturbance and underlying environmental gradients influenced the availability of establishment sites within canopy gaps and hence subsequent forest establishment. These results are considered in relation to patterns of forest succession and the coexistence of species in these forests.

CHAPTER II

LITERATURE REVIEW

Temperate rain forest communities dominated by the Podocarpaceae trees *Dacrycarpus dacrydioides*[1] (kahikatea), *Dacrydium cupressinum* (rimu), *Prumnopitys ferruginea* (miro), and the angiosperm *Weinmannia racemosa* (kamahi) cover extensive areas of the post-glacial outwash surfaces of south Westland (Wardle 1977; Norton & Leathwick 1989; Duncan *et al.* 1990, Appendix 1). These forests comprise a large proportion of the lowland indigenous forest remaining in New Zealand.

The outwash surfaces that support these communities lie in the troughs carved by Pleistocene glaciers. These surfaces have been formed from sediment deposited following glacial retreat, commencing about 14000 years ago (Suggate & Moar 1970). Large braided rivers draining from the western catchments of the Southern Alps flow across these outwash surfaces. Mean annual rainfall in upland catchments of the Southern Alps can exceed 11000 mm (Griffiths & McSaveney 1983). The combination of high rainfall and short, steep catchments result in a dynamic floodplain environment. Suspended sediment yields in south Westland rivers are about 10 times greater than world average rates for mountainous regions (Griffiths 1979) and most of this sediment is deposited during periodic flood events (Cowle 1957).

Flooded rivers that change course can destroy or damage areas of forest. Flooding causes tree mortality through physical damage and destruction, or as a consequence of sediment deposition. Observations of logs and stumps buried in alluvium, and stand mortality following inundation with silt, suggest that flooding is an important form

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[1]Nomenclature follows Allan (1961) with the recent taxonomic changes suggested by Connor & Edgar (1987).

of disturbance on lowland floodplains (Foweraker 1929; Wardle 1974). The largest stand of *Dacrycarpus dacrydioides* in Westland National Park (c. 400 ha) was inundated with gravel and silt to a depth of >1 m when the Cook River changed course during a flood in 1970 (Timmins & Norton 1988). Trees were destroyed during the flood and most of those left standing subsequently died.

The early stages of succession on exposed flood deposits were described by Wardle (1974, 1980a). Variation in drainage, soil texture, and topography result in multiple pathways of vegetation development (Wardle 1980a). However, stands dominated by *Dacrycarpus dacrydioides* commonly establish on flood deposits and are characteristic of recent, alluvial silt soils (Wardle 1977; Norton & Leathwick 1989; Duncan *et al.* 1990). Maintenance of *D. dacrydioides* at a site appears dependent on further flood disturbance (Wardle 1974).

With time, and in the absence of further openings formed by floods, *Dacrydium cupressinum* replaces *Dacrycarpus dacrydioides* as the dominant canopy tree (Wardle 1974, 1980a). On older outwash surfaces, undisturbed by flooding for long periods, *Dacrydium cupressinum* is the dominant canopy species with *Prumnopitys ferruginea* and *Weinmannia racemosa* prominent as subcanopy trees (Wardle 1977; Sowden 1986).

Mixed stands of *Dacrycarpus dacrydioides* and *Dacrydium cupressinum* are seen as an intermediate stage in a succession from *D. dacrydioides* to *D. cupressinum* dominated forest (Wardle 1977). This change in canopy dominance can occur within 3000 years of surface creation (Sowden 1986). The amount of time elapsed since flood disturbance is seen as an important determinant of forest composition. The distribution of forest types with differing proportions of *D. dacrydioides* and *D. cupressinum* has been related to surface age and susceptibility to flood disturbance (Wardle 1977, 1980a; Norton & Leathwick 1989; Duncan *et al.* 1990).

Succession from *Dacrycarpus dacrydioides* to *Dacrydium cupressinum* dominated forest parallels changes in soil properties associated with soil development through time (Sowden 1986). Soil drainage deteriorates, soil nutrient levels decline, and soil organic matter increases (Tonkin *et al.* 1985; Sowden 1986). Wardle (1974, 1980a) suggested that vegetation change may reflect declining soil fertility, caused by rapid leaching of nutrients in the high rainfall environment. Similarly, Hawkins & Sweet (1989) suggested that the distribution of *D. dacrydioides* and *D. cupressinum* could be explained in terms of their nutrient uptake characteristics.

Hawkins & Sweet (1989) measured seedling growth rates and levels of nutrient uptake over a range of nutrient supply levels. *D. dacrydioides* seedlings grew faster than *D. cupressinum* and had a disproportionately greater rate of growth at higher nutrient concentrations. *D. cupressinum* had a slower rate of growth but a greater efficiency of nutrient uptake at low levels of supply, which are characteristics that may give it a competitive advantage on nutrient-poor sites. Hawkins & Sweet (1989) suggested that forest composition is determined by soil nutrient status and the relative uptake ability of the tree species. *Dacrycarpus dacrydioides*, with a faster growth rate and greater uptake level at high nutrient concentrations, dominates on recent, fertile soils. *Dacrydium cupressinum* with a competitive advantage on nutrient-poor sites dominates on the older, less fertile surfaces.

A number of studies have shown a close relationship between vegetation pattern and soil properties in south Westland (Smith & Lee 1984; Sowden 1986; Norton & Leathwick 1990; Duncan *et al.* 1990). However, studies of stand dynamics have emphasised the importance of disturbance in influencing stand structure and composition. Limited size and age data show that relatively even-aged stands of *D. dacrydioides* establish after catastrophic floods and that little recruitment occurs in the absence of further major disturbance (Wardle 1974; Smale 1984; Robertson *et al.* 1986). *D.*

cupressinum has a similar pattern of group even-aged establishment in forests on older outwash surfaces (Six Dijkstra *et al.* 1985; B. Cornere *unpublished data*). However, in these forests regeneration of *D. cupressinum* occurs in openings formed by wind disturbance that can range in size up to 20 ha (Hutchinson 1932; Poole 1937; Six Dijkstra *et al.* 1985; Norton *et al.* 1988).

The studies reviewed here suggest that succession from *D. dacrydioides* to *D. cupressinum* dominated forest parallels a change in disturbance regime. In the absence of catastrophic flooding windthrow is the major stand initiating disturbance. The nature of the opening formed by different types of disturbance may therefore be an important determinant of subsequent forest establishment.

CHAPTER III

STUDY AREA

The six stands selected for study were all located on the floodplain of Ohinemaka Forest (43° 39′ S, 169° 32′ E) on the west coast of New Zealand's South Island (Fig 1). This area was selected for study because it possesses the following characteristics: (1) The area occurs in the 150 km long region of the South Islands' west coast in which *Nothofagus* species (southern beech) are absent. Forests on floodplains to the south of Ohinemaka have a significant component of *Nothofagus* that may influence patterns of succession (see for example Smith & Lee 1984); (2) The area has forest types representing the range of successional stages from *D. dacrydioides* to *D. cupressinum* dominated forest; (3) Apart from clearing for pasture around the upper reaches of the Ohinemaka River and across to Power Creek the forest has not been logged and the impact of humans in the area is minimal; (4) The area is relatively accessible; (5) The area is protected and forms part of the Southwest New Zealand World Heritage Park.

The floodplain of Ohinemaka Forest (c. 3400 ha) was formed in a glacial trough between the block of Palaeozoic greywacke and granite comprising the Paringa and Hunt hills to the west, and the Cretaceous sedimentary rocks and moraine deposits of Mt. Arthur to the east (Fig 1). It is bordered to the north by the Tasman Sea and to the south by the Douglas Range, forming part of the Southern Alps. The entire area lies close to sea level with the highest points occurring around the bases of the hills (up to 60 m a.s.l). Introduced deer and Australian brushtail opossums are present in low numbers throughout the study area.

Climate

The prevailing westerly winds and close proximity to the coast result in a mild,

equable climate. Mean annual precipitation at Haast (65 km southwest) is 3460 mm with only slight seasonal variation (Hessell 1982). Rainfall in the study area is likely to be 4000-5000 mm annually (Wardle 1980b). Mean annual temperature is c. 11.9°C with a January mean of 16.6°C and a July mean of 6.8°C (based on the equations of Norton 1985).

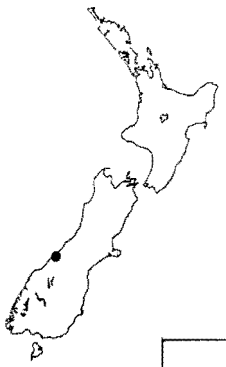
Geomorphology

The flat topography of the study area is a result of sediment deposition following glacial retreat and subsequent erosion of the surrounding uplands. Most of the floodplain was formed from river gravel deposits that are unlikely to be older than 6000 years and may be considerably younger (Mortimer *et al.* 1984). In the northeast there are extensive swamp deposits formed in an old lagoon (Wardle 1979; Mortimer *et al.* 1984). At present alluvial deposition occurs in the region of Power Creek and around the bases of the Paringa Hills and Douglas Range.

Vegetation

Five forest, one scrub, and two mire/swamp communities have been identified in the study area (Fig 2). The distribution of plant communities has been related to landform types and soil properties (Duncan *et al.* 1990, Appendix 1). Forest dominated by *Dacrycarpus dacrydioides* [(kahikatea)/*Cyathea* forest in Duncan *et al.* 1990] occurs between the Ohinemaka River and the base of the Paringa Hills on recent, well drained soils derived from alluvium. Mixed *D. dacrydioides*/*Dacrydium cupressinum* forest [(rimu)-(kahikatea)/(kamahi) forest in Duncan *et al.* 1990] occurs predominantly on moderately to well drained soils derived from alluvium in the south of the study area. *D. cupressinum* dominated forest [rimu/kamahi forest and rimu/*Neomyrtus* forest in Duncan *et al.* 1990] occurs on poorly drained soils derived from river gravel and swamp deposits in the north and east of the study area.

FIGURE 1: Map of the study area showing the main physiographic features and the locations of the six stands selected for study (K1, K2, F1, F2, M1, and M2 below).



Plot grid references: Infomap 260 G36, PARINGA.

K1 283 235, K2 328 208, F1 315 205, F2 307 188,

M1 & M2 338 217

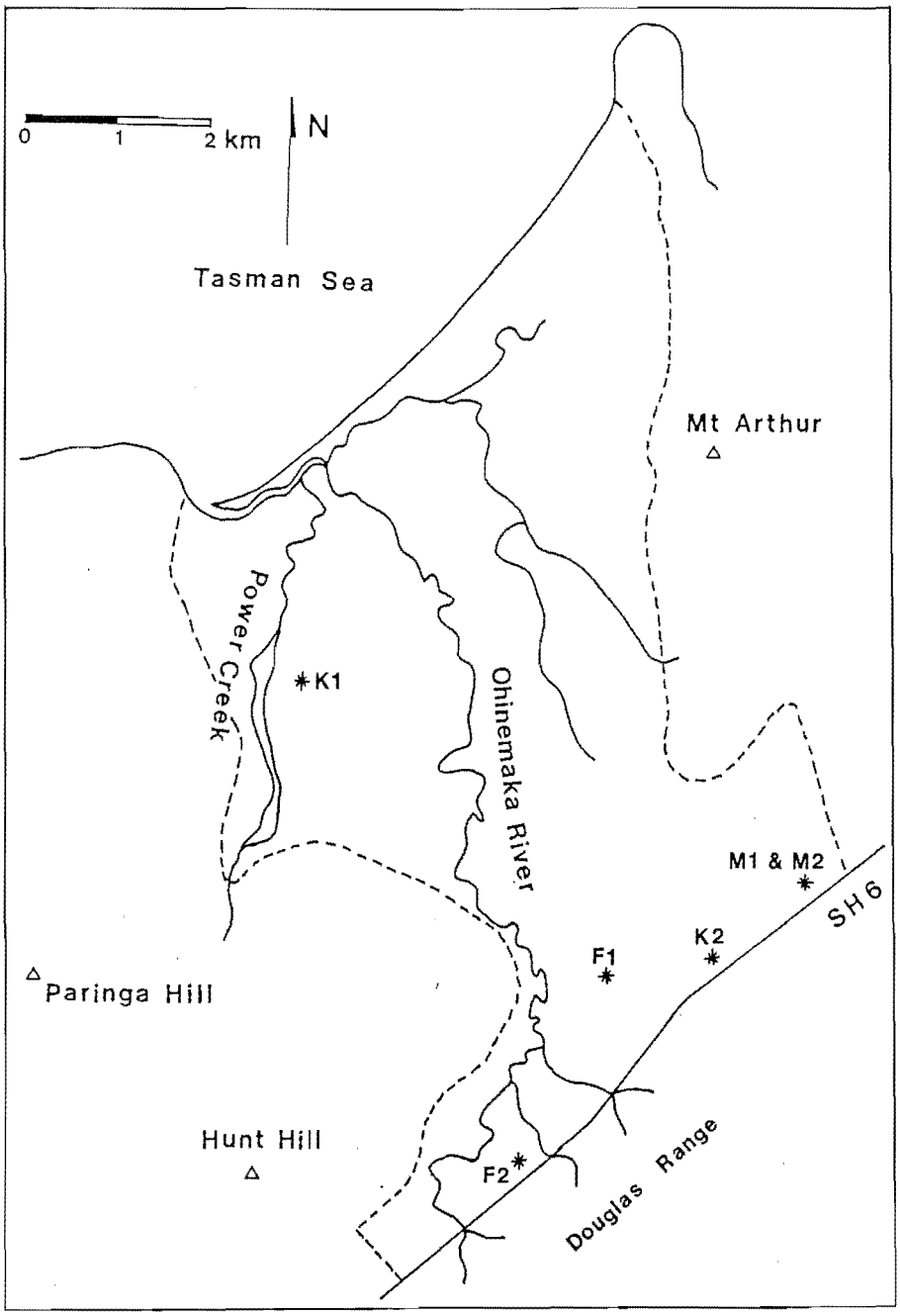
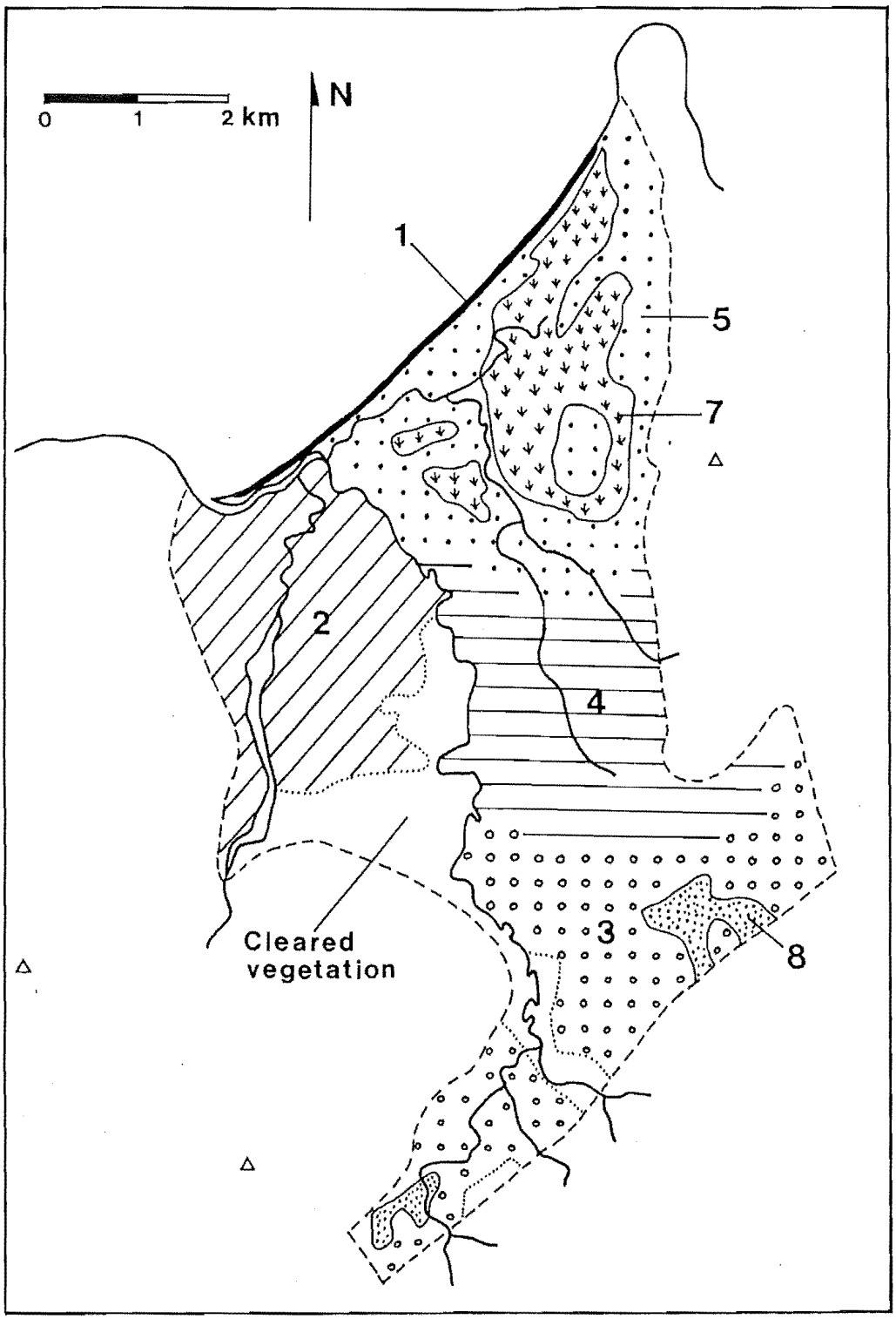


FIGURE 2: Vegetation map of the study area (from Duncan *et al.* 1990). The mapped communities are: 1. gorse scrub; 2. (kahikatea)/*Cyathea* forest; 3. (rimu)-(kahikatea)/(kamahi) forest; 4. rimu/kamahi forest; 5. rimu/*Neomyrtus* forest; 7. wire rush-*Juncus* rushland; 8. *Phormium* flaxland. [Kahikatea]/(*Myrsine*) forest is not mapped but occurs dispersed throughout the study area.



CHAPTER IV

METHODS

STAND SELECTION

Six forest stands differing in canopy composition and disturbance history were selected for study (Fig 1). Because one of the aims of this study was to examine the influence of disturbance on the patterns of forest succession stands that represent stages in development from *Dacrycarpus dacrydioides* to *Dacrydium cupressinum* dominated forest were selected. Two of the stands chosen for study were dominated by *D. dacrydioides* (stands K1 and K2) while the remaining four stands had mixed canopies of *D. dacrydioides* and *D. cupressinum*. Patterns of regeneration in *D. cupressinum* dominated forest have been described elsewhere (Hutchinson 1928, 1932; Poole 1937; Six Dijkstra *et al.* 1985; Baxter & Norton 1989; B. Cornere *unpublished data*).

This study also examines the influence of different types of disturbance on forest composition and structure. Soil profiles in four of the stands (K1, K2, F1 and F2) showed recent soils formed on alluvial silt or gravel. These profiles suggested the sites had been relatively recently affected by flood disturbance. The remaining two stands (M1 and M2) had well developed soil profiles that reflected longer periods of soil development in the absence of flooding. In these two stands scattered, large podocarps were emergent over a lower, regenerating tier of podocarps and broadleaved species. Large stumps and fallen logs in these stands suggested regeneration occurred in response to wind disturbance.

Rectangular sample plots of 0.18 - 0.54 ha were established in each of the six stands and all sampling was confined to these. Plots of varying size were used because

of different stem densities and to confine sampling to within the stand type selected for study. Each sample plot was divided into 30 x 30 m (0.09 ha) subplots and each subplot was gridded into 5 x 5 m contiguous quadrats.

Sampling was carried out from October 1988 to March 1989 and November 1989 to January 1990.

STAND STRUCTURE

Because there is often a weak relationship between tree diameter and age (Harper 1977) both size and age structure were used to reconstruct tree population dynamics in the six stands.

The diameter of all *Dacrycarpus dacrydioides*, *Dacrydium cupressinum*, *Prumnopitys ferruginea*, and *Weinmannia racemosa* trees ≥5 cm diameter was measured at 1.3 m above establishment height (dbh). Tree diameters were used to construct size-class frequency distributions. Because the size-class distributions were used to interpret population dynamics only the largest stem of multi-stemmed trees was measured. The diameter of all dead standing trees ≥5 cm dbh was measured and the trees were identified if possible. The numbers of saplings (≥1.3 m tall but <5 cm dbh) of all four species and the numbers of seedlings (≥0.5 m but <1.3 m tall) of *Dacrycarpus dacrydioides*, *Dacrydium cupressinum*, and *Prumnopitys ferruginea* were recorded.

To describe the vertical structure of the stands all trees ≥5 cm dbh were assigned to one of five relative height tiers: emergent over the canopy, upper main canopy, lower main canopy, subcanopy, or shrub tier.

Trees ≥5 cm dbh were cored with an increment corer at 1.3 m above their establishment height to determine tree age. Extensive buttressing around the bases of

trees prevented coring at a lower height. One to four cores (usually two) were extracted from each tree. Where possible extraction was along the longest radius to minimise errors due to missing rings (Duncan 1989, Appendix 2). When more than one core was extracted from a single tree the core with the greatest number of visible growth rings was used to estimate tree age.

Cores were air-dried, mounted, and then sanded using successively finer grades of sandpaper until the growth rings were visible. Growth rings were counted under reflected light using a binocular microscope. Franklin (1969) found evidence for annual growth ring formation in *Dacrydium cupressinum*. Annual growth ring formation has been demonstrated in a number of other lowland, New Zealand trees: *Agathis australis* (Palmer & Ogden 1983); *Beilschmiedia tawa* (Ogden & West 1981); *Phyllocladus trichomanoides* (Herbert 1977) and *Podocarpus hallii* (Wells 1972). Annual growth ring formation was therefore assumed for *Dacrycarpus dacrydioides*, *Prumnopitys ferruginea*, and *Weinmannia racemosa*.

The age of trees in which cores failed to reach the chronological centre (due to a rotten tree centre or a short increment core) were estimated by assuming that the chronological centre was at the trees geometric centre (see Norton *et al.* 1987). For the majority of trees cores missed the chronological centre but the arcs of the inner growth rings were visible. The age of the missing portion was estimated using the geometric model in Duncan (1989).

Because of the errors in estimating tree age using the method employed (Duncan 1989), and observations of missing rings in *Dacrycarpus dacrydioides* (Duncan 1989) and *Dacrydium cupressinum* (B. Cornere *unpublished data*), broad age-class intervals (25-50 years) were used in constructing age-class frequency distributions (see below). The precision of age estimates is likely to be greater in younger trees. All of the age estimates

presented in this study are at 1.3 m above the point of establishment. No corrections were made to allow for growth to coring height.

Age structures of the podocarp species in each plot were determined by the following two methods:

(1) The ages of all trees ≥5 cm dbh in a plot were estimated. Trees with rotten centres, large trees outside the range of the increment corer (>≈80 cm dbh), or small trees 5 - 7 cm dbh were often not cored. Ages of the uncored trees ≥5 cm dbh were estimated from best-fit regressions (either linear or log-log) of age against diameter for the aged trees in the plot. Age-class frequency distributions were constructed for all trees ≥5 cm dbh.

(2) In heavily populated stands a systematic sample of trees were cored. Trees ≥5 cm dbh were consecutively numbered during the measurement of tree diameters. Every third to fourth tree in the plot was then cored. The age-class frequency distribution constructed from the systematic sample of tree ages was then assumed to be the same as the age distribution of the larger population of trees in the plot.

Indistinct growth rings made accurate ageing of *Weinmannia racemosa* trees difficult so age structures were not determined for this species. Interpretation of *W. racemosa* population dynamics were based on size-class distributions and the degree to which diameter reflected age was assessed in plots with >20 *W. racemosa* trees. A sample of >20 trees, with at least two trees in each 5 cm diameter interval up to 40 cm dbh, were cored in each plot. Cores with growth rings which were too indistinct to count were discarded. The best-fit regression between age and diameter for the remaining cores was used as a measure of the relationship between size and age. This approach was also used to interpret the population dynamics of *Dacrycarpus dacrydioides* and *Dacrydium cupressinum* in stand M1 where over 80% of the trees were <15 cm dbh.

The relationship between size and age for species in each stand was assessed by calculating best-fit regressions (either linear or log-log) of age against diameter. An

estimate of mean radial growth rate for each cored tree was obtained by dividing tree radius by age.

SPATIAL DISTRIBUTION OF TREE AGES

Interpretation of age distributions often leads to the identification of even-aged stands or even-aged cohorts in all-aged stands (Lorimer 1985). The presence of even-aged patches of trees is often compelling evidence of past disturbance (Lorimer 1985). The size and distribution of such patches can be used to interpret disturbance history (Heinselman 1973; Henry & Swan 1974; Oliver & Stephens 1977; Stewart 1986a; Foster 1988). Even-aged patches of trees, however, may be indistinguishable in an age distribution if there are a number of differently-aged patches and the spread of ages in each patch overlap. For example, stands in which trees establish in small patches by colonisation of treefall gaps often have an all-aged distribution in which individual even-aged groups are indistinguishable (Hytteborn *et al.* 1987; Taylor & Qin Zisheng 1988; Stewart & Rose 1990). In such cases patterns of local even-aged establishment may be evident in the spatial distribution of tree ages. I therefore analysed the spatial distribution of tree ages with the aim of identifying even-aged patches of trees that established in localised disturbance openings.

The spatial locations of trees were needed in addition to tree ages. Live and dead standing trees of all four species, and seedlings and saplings of *D. dacrydioides*, *D. cupressinum*, and *P. ferruginea* were mapped as X, Y coordinates to the nearest 0.1 m in each 5 x 5 m quadrat. Multi-stemmed trees were recorded as a single point location measured at the centre of the tree clump. Coordinates in each 5 x 5 m quadrat were converted to a larger X, Y grid in each of the six sample plots.

If trees establish in even-aged patches then the spatial distribution of tree ages will

be non-random; trees of similar age will occur together. A variable such as tree age which exhibits such a spatial structure is said to be spatially autocorrelated. Measures of spatial autocorrelation can be used to test for significant pattern in the spatial distribution of a variable and to describe the pattern (Legendre & Fortin 1989).

Spatial autocorrelation

Measures of spatial autocorrelation can determine if neighbouring points are more or less similar to each other with respect to some variable (in this case tree age) than would be expected from a random distribution of the variate values. In this study 'neighbouring points' were defined using 3 m distance classes. The first distance class was 0 - 3 m, the second >3 - 6 m and so forth up to the length of the longest plot side. For each distance class *d* a pair of trees *i* and *j* were considered neighbours if they were within the distance apart pertaining to that distance class. Using this definition Moran's *I* coefficient (Moran 1950) was calculated as a measure of spatial autocorrelation for each distance class *d*:

$$I(d) = \frac{N\sum_i \sum_j w_{ij}(x_i-\bar{x})(x_j-\bar{x})}{W\sum_i (x_i-\bar{x})^2}$$

where

I(d) is the value of Moran's coefficient for distance class *d*

N is the total number of point locations

x_i ($i = 1,\ldots,N$) is the value of the variate at each of *N* point locations

w_{ij} = 1 if points *i* and *j* were neighbours in distance class *d*, and

0 otherwise

$W = \Sigma w_{ij}$

All summations were for *i* and *j* varying from 1 to *N* but excluded cases where $i = j$.

The assumption of randomization was used as a null hypothesis (Upton & Fingleton 1985, p. 152), whereby the observed variate values are distributed randomly among the fixed point locations. Under this null hypothesis Moran's *I* coefficient is asymptotically normal with an expected value $E[I(d)] = -(N - 1)^{-1} \approx 0$ (Cliff & Ord 1981). Values of $I(d) > E[I(d)]$ are termed positively spatially autocorrelated and indicate that locations a distance d apart tend to have similar values of the variate (ie. similar age). Negative spatial autocorrelation (values of $I(d) < E[I(d)]$) indicates that locations a distance d apart tend to have dissimilar values of the variate (ie. dissimilar age).

The significance of deviations from expectation in each distance class were tested by calculating the variance of $I(d)$ under the null hypothesis of randomization (see Appendix 3 for details). Standard normal deviates, $z(d)$, were calculated for each distance class:

$$z(d) = \frac{I(d) - E[I(d)]}{\sqrt{var[I(d)]}}$$

The 0.05, 0.01, and 0.001 significance levels of z are 1.96, 2.58 and 3.29 respectively. Distance classes that contained fewer than 20 pairs of neighbouring points were excluded from analyses because the assumption of normality may be invalid for small groups (Upton & Fingleton 1985).

Testing the significance of deviations from expectation for autocorrelation coefficients pertaining to each distance class does not provide a test of significance for the data set as a whole because the k tests are not independent (Sakai & Oden 1983). Therefore, for a given overall significance level α a global test was made. The data set as a whole had significant spatial structure if the value of Moran's *I* coefficient in at least

one distance class was significant at the α/k significance level (Legendre & Fortin 1989).

Variation in spatial autocorrelation among trees at different distances was examined by plotting values of $z(d)$ on the vertical axis against distance class d on the horizontal axis. The resulting correlograms provide a description of the spatial structure. Correlograms were analysed by examining their shape as characteristic shapes are associated with different types of spatial structure (Legendre & Fortin 1989). For example, if trees occur in even-aged patches then a correlogram of tree age should show significant positive autocorrelation in small distance classes reflecting the association of trees of similar age within patches.

Identification of patches

When the shape of the correlogram indicated the presence of a patch structure individual patches were identified using ordination and cluster analysis.

A measure of association c_{ij} was calculated between each pair of trees i and j (except for $i = j$) that reflected both spatial proximity and age similarity (Webster & Burrough 1972, Cliff *et al.* 1975):

$$c_{ij} = \lambda \frac{d_{ij}}{d_{max}} + (1-\lambda) \frac{a_{ij}}{a_{max}}$$

where

a_{ij} and d_{ij}	are the differences in age, and distances between trees i and j, respectively
a_{max} and d_{max}	are the greatest age difference, and greatest distance between a pair of trees, respectively
λ	is a constant ($0 \leq \lambda \leq 1$) that reflects the relative weighting assigned to distance versus age.

Distance and age were given equal weighting in calculating the association measures (ie. $\lambda = 0.5$). Values of c_{ij} range from >0 - 1, with smaller values indicating greater similarity.

Non-metric multi-dimensional scaling (as implemented in the package PATN, [Belbin 1989]) was used to arrange trees in two dimensions, from the matrix of association measures. Ordination diagrams, plotting tree positions on a 2-dimensional graph, were used to examine the relationships among trees and to identify clusters of points that may represent even-aged patches of trees.

In addition, agglomerative hierarchical clustering (UPGMA as implemented in the package PATN [Belbin 1989]) was used to group trees of similar age and spatial location from the matrix of association measures.

Groups of trees identified from either the ordination diagram or the dendrogram showing the clustering hierarchy were recognised as even-aged patches if they were spatially discrete, their age-structure indicated that they were relatively even-aged, and they were of different age to spatially adjacent groups.

SPATIAL PATTERNS

Spatial autocorrelation analysis, described above, deals with the distribution of a variable (such as tree age) in horizontal space. Also of interest is the distribution of the tree locations themselves. Are trees distributed randomly over a surface or do they tend to be grouped together (clumped distribution) or evenly-spaced out (regular distribution)? Similarly, are two groups of trees distributed randomly in space with respect to one another (independently distributed) or are they positively or negatively associated with each other?

The spatial patterning of vegetation may reflect a variety of processes. These include patterns of disturbance (Williamson 1975; Veblen *et al.* 1980), competition (Yeaton 1978; West 1984; Kenkel 1988), microhabitat availability (Mott & McComb 1974; Fowler & Antonovics 1981) and herbivory (Janzen 1970). Analysis of the spatial pattern of individual species, and spatial interactions among species may provide insight into some of these processes (Hatton 1989).

A common approach to the analysis of spatial pattern has been to map plants in contiguous quadrats. Various indices enable the observed distribution of the number of plants per quadrat to be compared with that expected from random. Pattern at different scales can be analysed by grouping neighbouring quadrats into larger blocks (Greig-Smith 1983).

The quadrat count approach has a number of disadvantages (Pielou 1977; Upton & Fingleton 1985), notably: (1) detection of pattern is limited to scales equal to the chosen quadrat size or multiples obtained by blocking quadrats, (2) tests of significance are often invalid because blocks obtained by combining quadrats at various scales are not independent (but see Mead 1974), and (3) choices in the starting point and in the orientation of blocks when quadrats are grouped affects the outcome (but see Hill 1973). While a number of methods have been developed that overcome specific problems no one method is entirely adequate (Upton & Fingleton 1985). The limitation to detection of pattern at scales greater than or equal to the quadrat size is inherent in this method.

An alternative approach involves mapping trees as point locations and comparing the distribution of distance measurements (usually plant-nearest plant or point-nearest plant) with the distribution expected from randomly dispersed trees (Clark & Evans 1954; Diggle 1983). However, this approach limits detection of pattern to scales in the region of nearest neighbour distances. Pattern at larger scales cannot be detected.

Recently, methods for analysing the spatial distribution of trees mapped as point locations that combine quadrat counting with distance measurement have been developed (Ripley 1976, 1977; Lotwick & Silverman 1982; Diggle 1983). These methods compare the distribution of all interplant distances with that expected from randomly dispersed trees. Pattern can be detected at a any scale up to half the length of the shortest side of a plot. This combined approach was used in the present study to analyse the spatial distribution of trees mapped as point locations.

Univariate spatial patterns (patterns of a single species or group) were analysed using the function *L(t)*, a transformation of the function *K(t)* (Ripley 1976, 1977), suggested by Besag (1977).

$$L(t) = \sqrt{\frac{K(t)}{\pi}} - t$$

The function *K(t)* uses all interplant distances to provide a measure of spatial pattern at various distances *t* (see Appendix 4 for details). Under the model of complete spatial randomness the function $L(t) = 0$. Values of $L(t) > 0$ indicate clumping at that distance t. Values of $L(t) < 0$ indicate a uniform distribution. Monte Carlo simulation was used to test the statistical significance of deviations of *L(t)* from 0 under the hypothesis of complete spatial randomness. Ninety-five percent confidence envelopes were generated from high and low values of the function *L(t)* obtained from 19 simulations of the random point process.

The function *L(t)* was also used to test the null hypothesis of random mortality based on the patterns of live and dead standing trees. The pre-mortality spatial pattern was obtained by computing values of *L(t)* for the combined live and dead standing trees. Random removal of the same number of presently dead trees was simulated 19 times to construct 95% confidence envelopes for the pattern expected from random mortality. The observed post-mortality pattern of live trees was compared with the pattern expected from

random mortality.

The bivariate function $L_{12}(t)$, a transformation of the function $K_{12}(t)$ (Lotwick & Silverman 1982), was used to analyse the spatial patterns of pairs of species point locations (see Appendix 4 for details).

$$L_{12}(t) = \sqrt{\frac{K_{12}(t)}{\pi}} - t$$

Under the model of spatial independence $L_{12}(t) = 0$. Values of $L_{12}(t) > 0$ indicate positive association (attraction) between a pair of species point locations at that distance t. Values of $L_{12}(t) < 0$ indicate a negative association (repulsion). Monte Carlo simulation was used to test the statistical significance of deviations of $L_{12}(t)$ from 0 under the null hypothesis of spatially independent components (ie. no spatial association). Ninety-five percent confidence envelopes were generated from high and low values of the function $L_{12}(t)$ obtained from 19 toroidal shifts of one species with respect to the other (see Lotwick & Silverman 1982; Upton & Fingleton 1985, pages 253-254).

ESTABLISHMENT SITE PREFERENCES

To assess if different species preferred different sites for regeneration the establishment sites of all trees ≥5 cm dbh and *D. dacrydioides*, *D. cupressinum*, and *P. ferruginea* seedlings and saplings were recorded. Establishment was recorded as occurring on one of three site types: depression (sites where the water table was usually above the ground surface), level (sites on the forest floor), or elevated (raised sites on fallen logs, stumps, trunk buttresses or root plate mounds). For trees established on elevated sites height of establishment above the forest floor was recorded in one of three height classes (<0.5 m, 0.5 - 1 m, <1 m).

Establishment on elevated sites was often inferred from evidence such as stilt

roots, or tree fern trunks around which the roots and bole of *W. racemosa* trees that previously established epiphytically had coalesced. Because such evidence can disappear with time the proportion of older trees established in depressions or on elevated sites may have been underestimated. The establishment sites of seedlings and saplings were more readily apparent from direct observation. Because of this, data for trees ≥5 cm dbh, and seedling and sapling establishment site types were analysed separately.

To determine the relative proportions of the three site types available for establishment in each plot 25 point locations were systematically located within each 30 x 30 m subplot (50 - 150 point locations per plot) at the intersections of the 5 x 5 m grids. Each point location was recorded as either depression, level, or elevated.

To assess the importance of openings in the overstorey for tree regeneration the overhead cover above each tree ≥5 cm dbh, and seedlings and saplings of *D. dacrydioides*, *D. cupressinum*, and *P. ferruginea* was recorded in one of three classes: (1) open (≥⅔ of the trees crown was in the open with no direct overhead cover); (2) intermediate (⅓-⅔ of the trees crown was in the open with no direct overhead cover); (3) closed (the tree occurred beneath a closed canopy or ≤⅓ of the trees crown was in the open).

DISTURBANCE HISTORY

At least two soil profiles, from soil pits or stream bank cuttings, were examined in each plot. The type and depth of underlying sediments and the stage of soil development gave an indication of the flood history of the stands. Soil profiles in the four recently flooded stands were very weakly developed and trees in these stands had established on deep alluvial silt and fine river gravel deposits, suggesting recent flood disturbance. Soil profiles in the remaining two stands were well developed and reflected longer periods of

soil development in the absence of flood disturbance. In addition, information on: (1) the temporal patterns of tree establishment, (2) the spatial arrangement of tree ages, and (3) tree establishment sites and the abundance of woody debris on the forest floor, was used to reconstruct disturbance history in the six stands.

CHAPTER V

RESULTS

DACRYCARPUS DACRYDIOIDES FOREST ESTABLISHED AFTER FLOODING

STAND K1

Stand structure and spatial distribution of tree ages

Dense, thin-crowned *Dacrycarpus dacrydioides* trees 30 - 35 m tall formed the canopy of stand K1 (Table 1). The subcanopy tiers (<15 m tall) were dominated by broadleaved species such as *Carpodetus serratus*, *Pennantia corymbosa*, and scattered *Weinmannia racemosa*.

The age structure of *Dacrycarpus dacrydioides* trees in stand K1 was determined by systematically ageing a sample of trees. In one half of the plot every second consecutive tree and in the second half every fourth tree was cored. A total of 112 trees were aged.

Size and age distributions showed that *Dacrycarpus dacrydioides* trees in stand K1 were relatively even-aged (Fig 3a,b). The bell-shaped age distribution suggested that establishment began after disturbance 450 - 500 years ago, reached a peak c. 300 years ago, and then declined as regeneration was inhibited by the growth of canopy trees. Seedlings and saplings of *D. dacrydioides* were rare and no recruitment into the canopy had occurred in the last 100 years. Dead standing *D. dacrydioides* trees in the smaller size classes were common (Fig 3c) and may reflect self-thinning caused by density dependent mortality. Recruitment of trees into the canopy occurred over a long time period (c. 300 - 400 years).

TABLE 1: Number of trees ≥5 cm dbh in relative height classes, basal area, and density for the four main tree species in the six study plots. 1 = emergent, 2 = upper main canopy, 3 = lower main canopy, 4 = subcanopy, 5 = shrub tier, BA = basal area (m^2/ha), DEN = density (Number of stems/ha), - indicates tier was not recognised in that plot.

Plot (dimensions) *Species*	1	2	3	4	5	BA	DEN
K1 (60x60m)							
D.dacrydiodes	-	166	108	23		109.0	825
D.cupressinum	-		1			.1	3
P.ferrugineus	-			1		.01	3
W.racemosa	-			7	2	.4	25
K2 (60x60m)							
D.dacrydioides	-	75	78	7		95.4	444
D.cupressinum	-		4			1.1	11
P.ferrugineus	-			3	11	.6	39
W.racemosa	-			163	26	21.5	525
F1 (60x60m)							
D.dacrydioides	-	141	26	3		46.2	472
D.cupressinum	-	87	68	13		26.5	467
P.ferrugineus	-	1	12	5		1.6	50
W.racemosa	-	14	111	21	2	11.7	411
F2 (90x60m)							
D.dacrydioides	-	38	10			36.5	89
D.cupressinum	-	17	15	6		15.0	70
P.ferrugineus	-	3	16	23	7	3.4	91
W.racemosa	-		73	35	3	15.8	206
M1 (60x30m)							
D.dacrydioides	1	37	106	-	25	14.9	939
D.cupressinum	7	29	20	-	6	36.6	344
P.ferrugineus	6	13	20	-	11	8.9	278
W.racemosa		3	47	-	21	9.5	394
M2 (60x30m)							
D.dacrydioides	2	21	13	-		3.3	200
D.cupressinum	9	28	27	-	1	21.3	361
P.ferrugineus	1	15	39	-	2	7.9	317
W.racemosa		32	31	-	1	23.3	356

FIGURE 3: Size- and age-class frequency distributions for the main species in stand K1. n = number of trees. Size classes are: Sd = seedlings (≥0.5 m but <1.3 m tall); S = saplings (≥1.3 m tall but <5 cm dbh); 1 = 5 - 14.5 cm dbh; 2 = 15 - 24.5 cm dbh; 3 = 25 - 34.5 cm dbh etc.

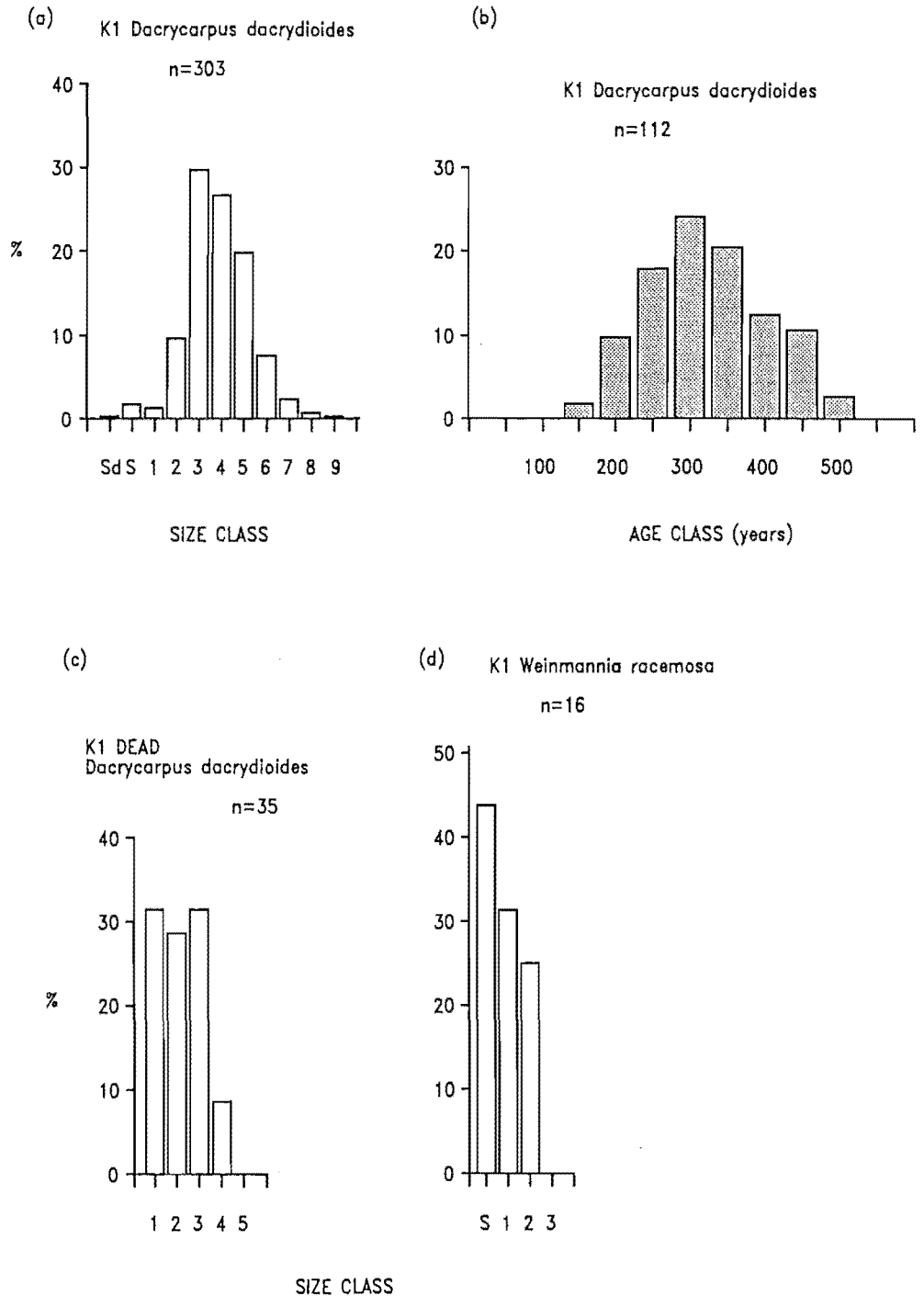


FIGURE 4: Spatial correlogram of *Dacrycarpus dacrydioides* tree ages in stand K1. Each distance class is a 3 m interval. Dotted lines indicate the 0.05 significance level.

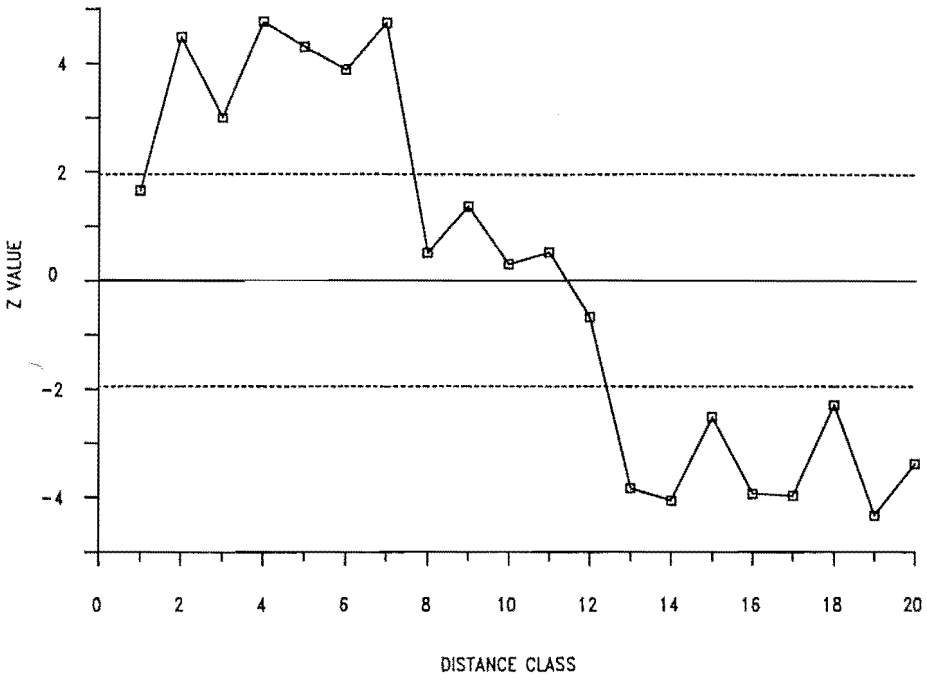
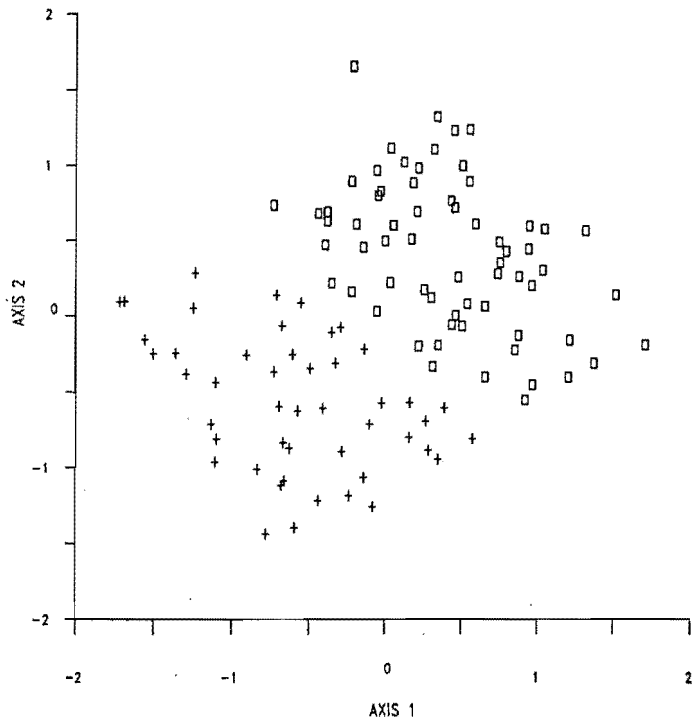


FIGURE 5: Scatter diagram obtained from an ordination of the association measure c_{ij}, reflecting tree age differences and spatial proximity, for the aged *Dacrycarpus dacrydioides* in stand K1. The two groups identified in the cluster analysis are shown in the diagram (+ and □) and correspond to the cohorts shown in Figure 6.



The distribution of *Dacrycarpus dacrydioides* tree ages had a significant spatial structure; the correlogram of tree age (Fig 4) was globally significant at the $\alpha = 0.05$ level. The shape of the spatial correlogram suggested there were two patches of even-aged trees in the plot. Significant positive autocorrelation in distance classes 2 - 7 (>3 - 21 m) was attributed to the association of similar aged trees within a patch. Significant negative autocorrelation in distance classes 13 - 20 (>36 - 60 m) reflected differences in age among trees in different patches.

There were no obvious clusters of points in the ordination diagram (Fig 5) that could represent distinct patches. However, two groups of relatively even-aged trees (K1W, Fig 6a,b and K1E, Fig 6c,d) were recognised from the cluster analysis. These two groups are represented by different symbols in the ordination diagram. The age distributions of these two groups of trees overlapped but were significantly different (two-tailed Kolmogorov-Smirnov test = 0.81, $P < 0.001$). Furthermore, each group of trees had established in a different part of the plot. Stand K1 was therefore composed of two relatively even-aged patches of trees that originated at different times (Fig 6). Because the recruitment intervals of the two patches overlapped they were not evident as distinct cohorts in the overall stand age distribution (Fig 3b).

Moran's *I* coefficient was calculated for tree ages in each of the two recognised patches to determine if smaller-scale patchiness was present. In both cases the test of global significance failed to exceed the $\alpha = 0.05$ level and the shape of the spatial correlograms did not indicate a patch structure. However, small groups of even-aged trees may have been undetected because only every second or fourth tree was cored and most of the trees aged were not adjacent neighbours.

Trees in the two patches had different radial growth rates. The mean ring width of *D. dacrydioides* trees in the younger patch, K1E (0.76 ± 0.28 mm) was significantly

FIGURE 6: Stem maps (a and c) and age-class frequency distributions (b and d) for the two *Dacrycarpus dacrydioides* cohorts identified in stand K1 from analysis of the spatial distribution of tree ages. n = number of trees.

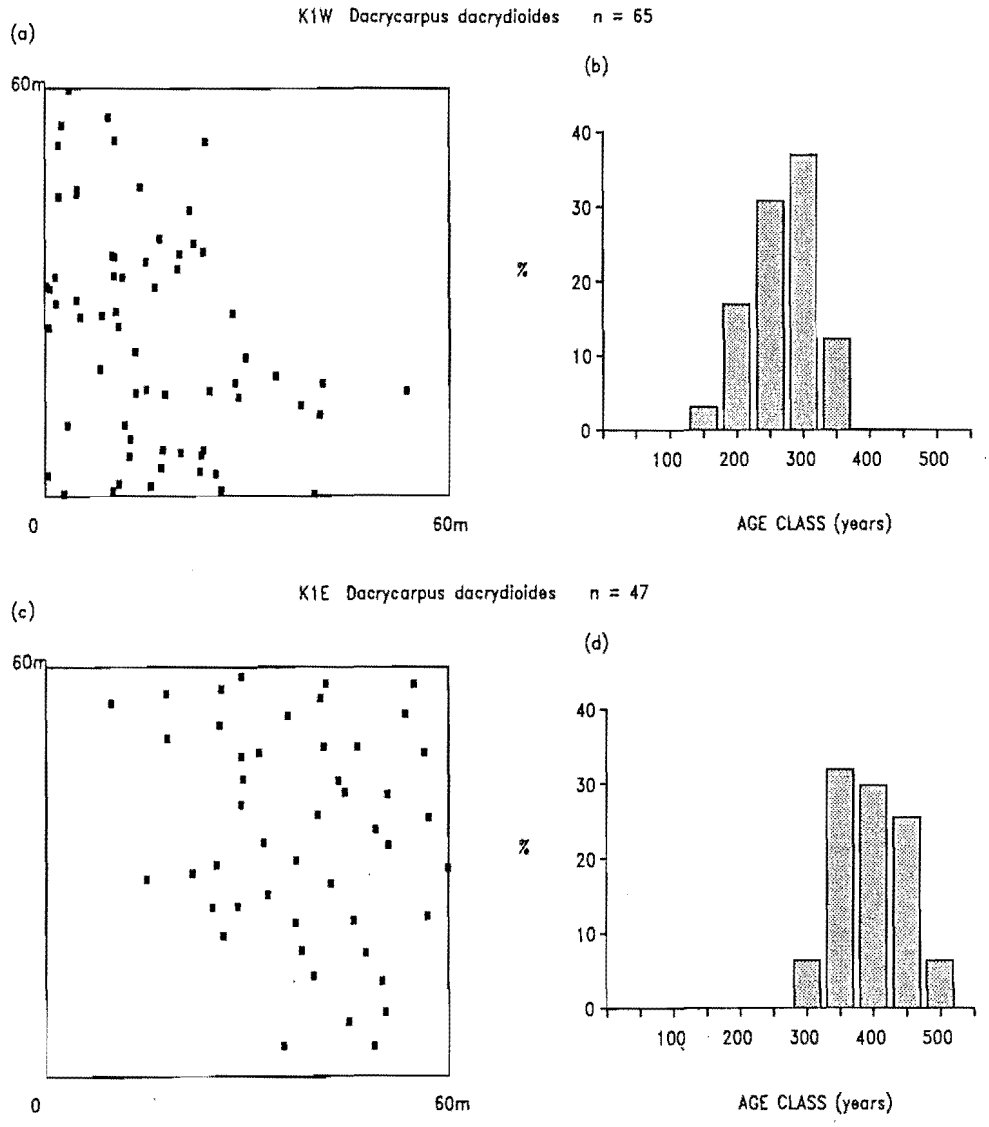


TABLE 2: Best-fit regressions of tree age at 1.3 m and diameter at 1.3 m, and mean annual ring widths of the aged trees in each of the six plots. Sample = the sampling method used to select trees for ageing: S = a systematic sample of trees were cored, A = all trees possible were cored, R = a sample of trees in the range of size-classes were cored; Y is age in years and X is diameter in cm; n = the number of trees aged; MRW = the mean annual ring width (in mm) ± standard deviation, calculated by dividing tree radius by age.

Plot	Sample	n	Equation	r^2	*P*	MRW(mm)
Species						
D. dacrydioides						
K1	S	112	$\log_e Y = 4.208 + .404 \log_e X$	.30	.000	0.67±0.25
K2	S	51	$\log_e Y = 4.245 + .422 \log_e X$	.53	.000	0.69±0.19
F1	S	70	$\log_e Y = 3.655 + .418 \log_e X$	.69	.000	0.96±0.27
F2	A	35	$Y = 66.647 + 3.319X$	.58	.000	1.10±0.29
M1	R	27	$\log_e Y = 3.704 + .343 \log_e X$	.77	.000	0.71±0.20
M2	A	31	$\log_e Y = 3.779 + .265 \log_e X$	.28	.002	0.78±0.32
D. cupressinum						
F1	S	78	$\log_e Y = 4.086 + .329 \log_e X$	.59	.000	0.73±0.23
F2	A	35	$\log_e Y = 3.418 + .527 \log_e X$	.70	.000	0.93±0.39
M1	R	19	$Y = 71.687 + 4.321X$	.88	.000	0.65±0.28
M2	A	54	$\log_e Y = 3.731 + .425 \log_e X$	.57	.000	0.58±0.29
P. ferrugineus						
F1	A	13	$Y = 98.386 + 3.29X$	.66	.001	0.60±0.17
F2	A	40	$\log_e Y = 3.446 + .535 \log_e X$	.72	.000	0.61±0.25
M2	A	43	$Y = 69.778 + 4.467X$	.72	.000	0.49±0.18
W. racemosa						
K2	R	19	$\log_e Y = 3.267 + .545 \log_e X$	.74	.000	0.72±0.20
F1	R	19	$\log_e Y = 3.556 + .394 \log_e X$	.32	.011	0.79±0.23
F2	R	23	$\log_e Y = 2.602 + .742 \log_e X$	.79	.000	0.81±0.22
M2	R	20	$\log_e Y = 3.320 + .535 \log_e X$	.68	.000	0.66±0.22

FIGURE 7: Relationship of age to diameter at 1.3 m (dbh) for the two *Dacrycarpus dacrydioides* cohorts (K1E and K1W in Figure 6) in stand K1. The regression equations are: K1E $\log_e$(age) = 4.84 + 0.291 $\log_e$(dbh), n = 47, r^2 = 0.28, P = 0.0001; K1W $\log_e$(age) = 4.39 + 0.309 $\log_e$(dbh), n = 65, r^2 = 0.42, P = 0.0000.

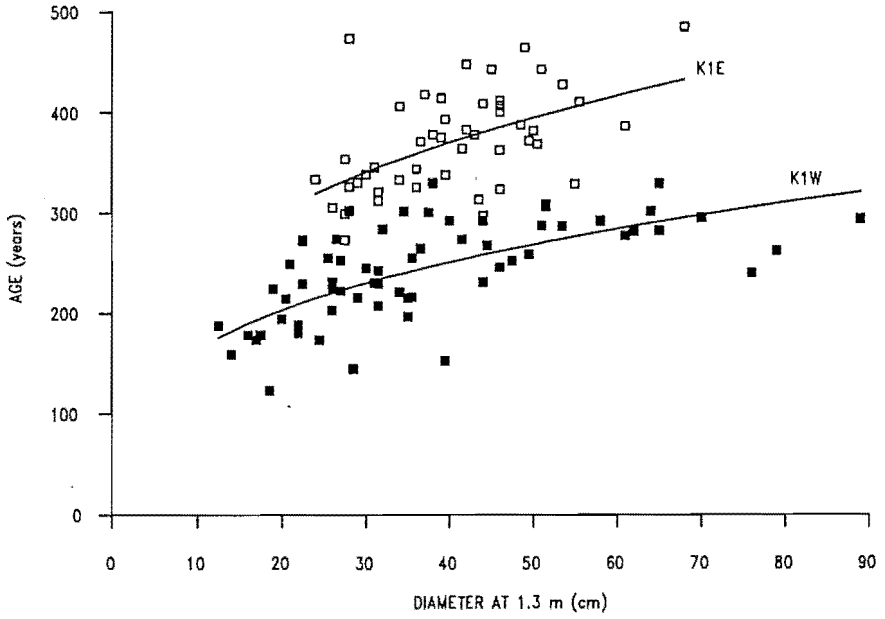
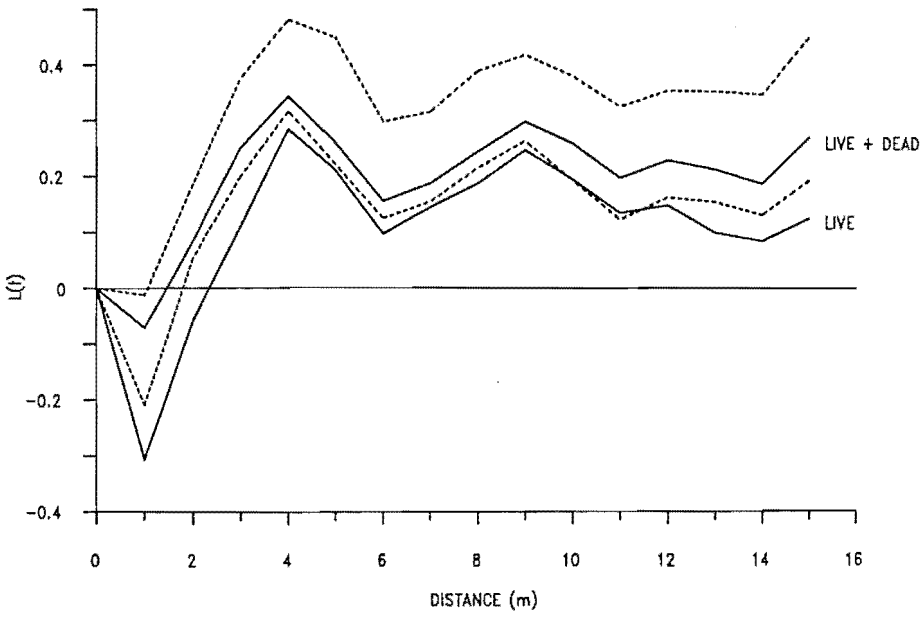


FIGURE 8: The function *L(t)* for *Dacrycarpus dacrydioides* ≥5 cm dbh in stand K1, with the post mortality pattern (live stems) tested against the null hypothesis of random mortality in the pre-mortality distribution (live + dead stems). 95% confidence envelopes (dotted lines) show the pattern expected after random mortality.



greater than for trees in the older patch, K1W (0.55 ± 0.11 mm) (t-test = 4.85, $P < 0.001$). The poor relationship between diameter and age for *D. dacrydioides* in stand K1 (Table 2) was in part due to the combination of two distinct cohorts with different growth rates (Fig 7).

The small number of subcanopy *Weinmannia racemosa* (Table 1) and their restriction to small size classes (Fig 3d) suggested that *W. racemosa* had only recently established in the stand. Only one *Prumnopitys ferruginea* and one *Dacrydium cupressinum* tree occurred in the plot (Table 1).

Regeneration patterns

Only 1% of *Dacrycarpus dacrydioides* established on elevated sites, the majority established on the ground (Table 4). In contrast over 80% of *Weinmannia racemosa* established on elevated sites, and 67% occurred in the open overhead cover class (Table 4), suggesting that openings in the overstorey were important for *W. racemosa* regeneration. The scarcity of *W. racemosa* in stand K1 may reflect the lack of suitable elevated establishment sites (Table 3).

Disturbance history

The arrangement of trees in two relatively even-aged patches suggested there were two disturbance events that initiated establishment of *Dacrycarpus dacrydioides*. The plot was located about 200 m from an actively flooding creek. Soil profiles throughout the plot revealed weakly developed, recent soils formed on alluvial silt up to 1.5 m deep. These profiles suggested that past flood disturbance initiated establishment of the younger and probably the older cohort of *D. dacrydioides*. The oldest tree aged in the older cohort was 485 years while the oldest tree aged in the younger cohort was 330 years.

Most *D. dacrydioides* established directly onto the flood deposit. There was no

evidence of prior occupation of the area and elevated sites, formed mainly by fallen trees, covered only 9% of the ground surface (Table 3). Dead trees were of small diameter and appeared to have originated from the present stand.

The site was well drained but numerous old and active stream channels dissected the plot, resulting in 20% of the sample points being classified as depressions (Table 3).

Spatial Patterns

Dacrycarpus dacrydioides ≥5 cm dbh were uniformly or randomly distributed at distances up to 3 m apart (Table 5). The hypothesis that non-random mortality resulted in more uniformly distributed trees was tested by comparing the post-mortality pattern with that expected by random removal of trees from the pre-mortality pattern (see Methods, page 25). There was a significant ($P < 0.05$) pattern of non-random mortality (Fig 8) suggesting that self-thinning resulted in uniformly or randomly distributed trees at small distances.

TABLE 3: Percentage of different site types in the six study plots. D = depression, L = level, E = elevated, n = number of point locations measured.

PLOT	D	L	E	n
K1	20	71	9	100
K2	10	43	47	100
F1	3	60	37	100
F2	0	54	46	150
M1	32	32	36	50
M2	6	56	38	50

TABLE 4: Percentage of trees (by species and size-class) in establishment site and overhead cover classes for stand K1. D = depression, L = level, E = elevated, C = closed, I = intermediate, O = open. Sd+S = seedlings + saplings. n = number of trees measured. Only size-classes with >5 individuals are included.

	Establishment site			Overhead cover			
	D	L	E	C	I	O	n
D.dacrydiodes							
≥5 cm dbh	1	98	1	6	20	74	297
Sd+S	0	100	0	67	33	0	6
W.racemosa							
≥5 cm dbh	0	11	89	11	22	67	9

TABLE 5: Patterns of spatial dispersion for *D. dacrydioides* trees ≥5 cm dbh in stand K1. Letters indicate significant ($P < 0.05$) deviation from a random distribution at distance t based on values of the function *L(t)*; U = uniform distribution, C = clumped distribution, . = random. n = number of trees.

	t (metres)				n
	1	5	10	15	
D.dacrydioides					
≥5 cm dbh	U . .	C C .	C .	C C C C . . .	297

STAND K2

Stand structure and spatial distribution of tree ages

Dacrycarpus dacrydioides 35 - 40 m tall dominated the canopy of stand K2 (Table 1). The density of *D. dacrydioides* ≥5 cm dbh was almost half that of stand K1 but a smaller difference in basal area indicated that trees in stand K2 were of greater mean diameter. The lower density, thin-crowned *D. dacrydioides* formed a relatively open canopy. *Weinmannia racemosa* dominated the sub-canopy (15-20 m) with their crowns filling the openings between *D. dacrydioides* trees.

The age structure of *Dacrycarpus dacrydioides* in stand K2 was determined by systematically coring a sample of 51 trees. Normally distributed size and age-class distributions suggested recruitment of *D. dacrydioides* occurred after catastrophic disturbance 450-500 years ago (Fig 9a,b). The age of the oldest tree cored (476 years) indicated the stand originated at about the same time as the oldest cohort in stand K1. Seedlings and saplings of *D. dacrydioides* were common in stand K2 but all were <1 cm dbh. Little recruitment of *D. dacrydioides* into the canopy had occurred in the last 200 years; only one of 51 aged trees was <200 years old. Dead standing *D. dacrydioides* in the smaller size classes were common (Fig 9c) and may reflect self-thinning caused by density dependent mortality.

Ages of the 51 cored *D. dacrydioides* were significantly positively autocorrelated in distance class 2 (>3 - 6 m). However, the spatial correlogram of tree age (Fig 10) was not globally significant at the $\alpha = 0.05$ level. Furthermore, the shape of the correlogram did not indicate a patch structure in the distribution of tree ages. The stand may have originated as a single cohort as there was no evidence of different-aged patches of trees that would suggest establishment in more than one disturbance opening. However, small groups of even-aged trees may have been undetected because a systematic sample of

FIGURE 9: Size- and age-class frequency distributions for the main species in stand K2. n = number of trees. Size classes are: Sd = seedlings (≥0.5 m but <1.3 m tall); S = saplings (≥1.3 m tall but <5 cm dbh); 1 = 5 - 14.5 cm dbh; 2 = 15 - 24.5 cm dbh; 3 = 25 - 34.5 cm dbh etc.

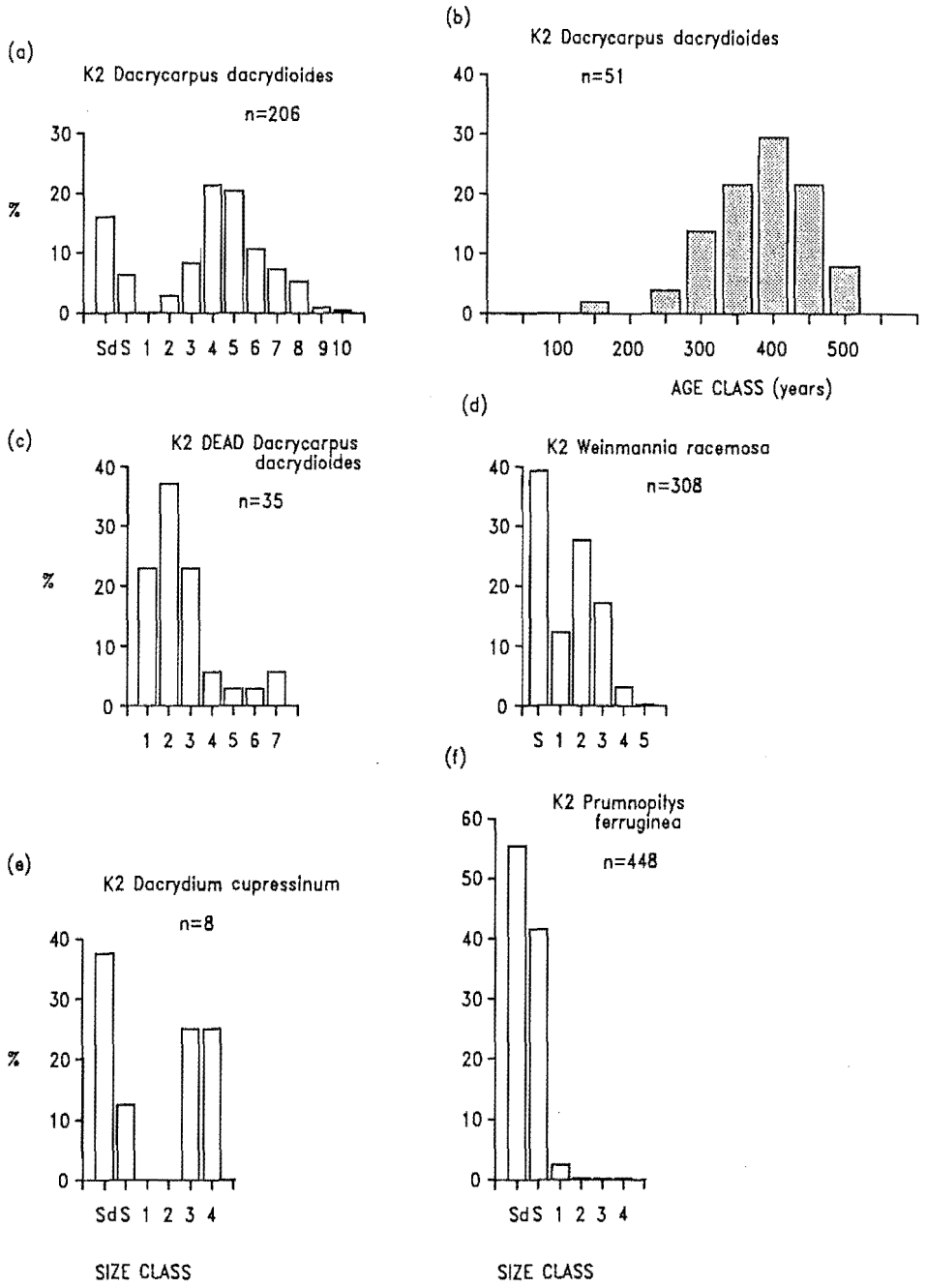


FIGURE 10: Spatial correlogram of *Dacrycarpus dacrydioides* tree ages in stand K2. Each distance class is a 3 m interval. Dotted lines indicate the 0.05 significance level.

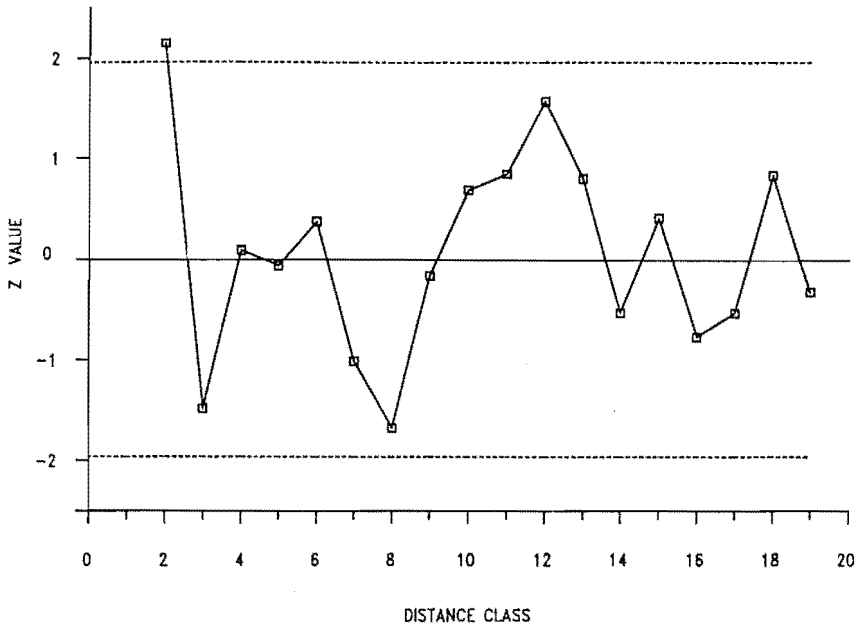
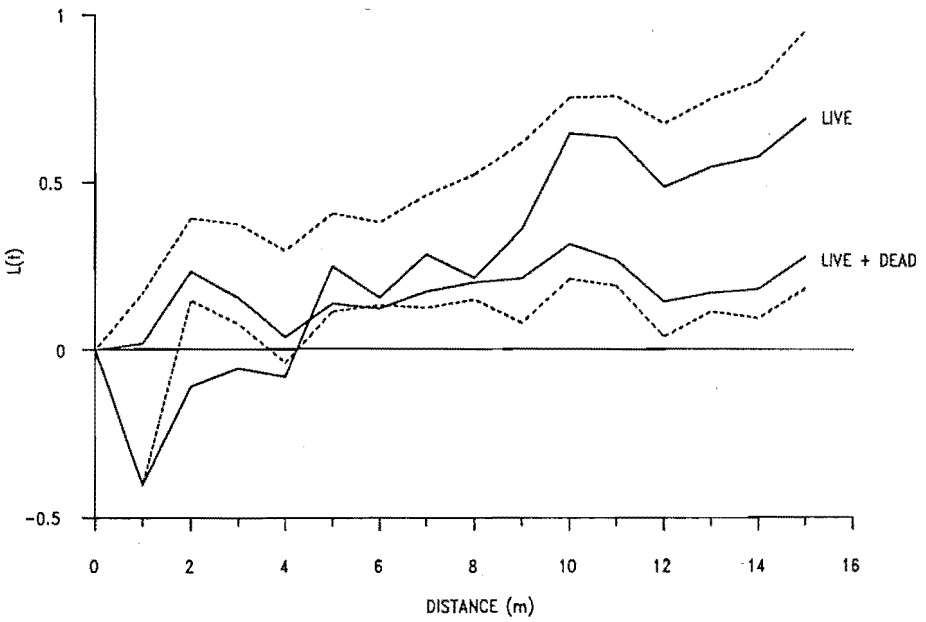


FIGURE 11: The function *L(t)* for *Dacrycarpus dacrydioides* ≥5 cm dbh in stand K2, with the post-mortality pattern (live stems) tested against the null hypothesis of random mortality in the pre-mortality distribution (live + dead stems). 95% confidence envelopes (dotted lines) show the pattern expected after random mortality.



trees were cored and most of the trees aged were not adjacent neighbours.

Weinmannia racemosa occurred abundantly as saplings and was present in all size-classes <55 cm dbh (Fig 9d). However, there were a large number of individuals 15-34.5 cm dbh that probably established in response to a disturbance event.

A single pulse of *Dacrydium cupressinum* regeneration occurred in stand K2, with the four trees ≥5 cm dbh occurring in a narrow range of size classes (Fig 9e). Three of these trees were cored and their ages ranged from 159-185 years. No recruitment of *D. cupressinum* into the canopy had subsequently occurred and only four seedlings and saplings <1 cm dbh were present in the plot.

Prumnopitys ferruginea occurred abundantly as seedlings and saplings (Fig 9f). There were, however, few trees ≥15 cm dbh suggesting only occasional recruitment into larger size-classes or recent establishment of *P. ferruginea* in the stand.

Regeneration patterns

Only 1% of *D. dacrydioides* trees ≥5 cm dbh established on elevated sites, the majority established on the ground (Table 6). In contrast, elevated sites were important for *Weinmannia racemosa* and *Prumnopitys ferruginea* establishment. Over 94% of all *P. ferruginea* and 81% of *W. racemosa* trees ≥5 cm dbh established on elevated sites.

Openings in the overstorey appeared important for successful recruitment of *W. racemosa* but were less important for *P. ferruginea.* Sixty one percent of *W. racemosa* trees ≥5 cm dbh, compared with only 21% of *P. ferruginea* ≥5 cm dbh, occurred in the open overhead cover class (Table 6).

TABLE 6: Percentage of trees (by species and size-class) in establishment site and overhead cover classes for stand K2. D = depression, L = level, E = elevated, C = closed, I = intermediate, O = open. Sd+S = seedlings + saplings. n = number of trees measured. Only size-classes with >5 individuals are included.

	Establishment site			Overhead cover			
	D	L	E	C	I	O	n
D.dacrydioides							
≥5 cm dbh	2	97	1	1	14	85	160
Sd+S	4	94	2	61	39	0	46
P.ferrugineus							
≥5 cm dbh	0	0	100	50	29	21	14
Sd+S	0	6	94	75	24	1	434
W.racemosa							
≥5 cm dbh	0	19	81	8	31	61	189

Disturbance history

Stand K2 was located at the base of the front range of the Southern Alps. Soils in the plot were recent and formed on alluvial silt and fine gravel which suggested the site had been flooded. The normally distributed age-class distribution and evidence of past flooding suggested that *D. dacrydioides* trees in stand K2 established following catastrophic flood disturbance.

The abundance of *Weinmannia racemosa* trees 15-34.5 cm dbh suggested a period of increased establishment in response to a further disturbance event. The regression between size and age for *W. racemosa* in stand K2 (Table 2) gave an age of 182 years for a 35 cm diameter tree. The range in ages of the three cored *Dacrydium cupressinum* trees (159-185 years) suggested they established in response to the same disturbance event.

Elevated sites covered about 47% of the surface of stand K2 (Table 3). These elevated sites included fallen logs and stumps, surface roots of *D. dacrydioides*, and large mounds of accumulated material around the bases of *D. dacrydioides* trees. The fallen logs all appeared to have originated from the present stand. Moreover, material around the bases of *D. dacrydioides* trees suggested that many of the elevated sites were formed after *D. dacrydioides* establishment.

Spatial Patterns

Non-random patterns of mortality for *D. dacrydioides* ≥5 cm dbh suggested that self-thinning resulted in uniform or randomly dispersed trees at distances up to 8 m (Fig 11, Table 7).

Clumping of *D. dacrydioides* and *P. ferruginea* seedlings and saplings (Table 7) reflected the patchiness of preferred establishment sites. *D. dacrydioides* seedlings and

saplings established on level sites and were clumped around the edges of small stream channels while *P. ferruginea* established in patches on elevated sites (Table 6).

Clumping of *W. racemosa* trees ≤20 cm dbh can be attributed to establishment in patches on elevated sites, and in small canopy openings. *W. racemosa* >20 cm dbh were randomly dispersed at distances up to 20 m. The majority of *W. racemosa* >20 cm dbh comprised the even-sized cohort that established contemporaneously with four *D. cupressinum* trees. Their random spatial distribution suggests that the disturbance event that initiated establishment of *D. cupressinum* and *W. racemosa* formed scattered openings throughout the stand.

The patchiness of different microsites as preferred establishment sites was reflected in significant spatial associations among size-classes (Table 8). *D. dacrydioides* seedlings and saplings were negatively associated with *P. ferruginea* seedlings and saplings, and *W. racemosa* trees >20 cm dbh. *D. dacrydioides* established primarily on level sites while *P. ferruginea* and *W. racemosa* established on elevated sites (Table 6). Furthermore, accumulated material around the bases of many *D. dacrydioides* trees had formed mounds. These elevated sites were apparently unsuitable for subsequent *D. dacrydioides* establishment but provided suitable sites for *P. ferruginea* and *W. racemosa*. This was reflected in positive associations between *D. dacrydioides* trees ≥5 cm dbh, *P. ferruginea* seedlings and saplings, and *W. racemosa* trees >20 cm dbh, and negative associations with *D. dacrydioides* seedlings and saplings.

Large (>20 cm dbh) and small (≤20 cm dbh) *W. racemosa* were negatively associated. Synchronous establishment of the larger trees in openings formed by disturbance would exclude further recruitment at those sites. Subsequent *W. racemosa* regeneration (trees ≤20 cm dbh) occurred in canopy openings in other parts of the stand.

TABLE 7: Patterns of spatial dispersion for trees (by species and size-class) in stand K2. Letters indicate significant ($P < 0.05$) deviation from a random distribution at distance t based on values of the function $L(t)$; U = uniform distribution, C = clumped distribution, . = random. Sd+S = seedlings + saplings, n = number of individuals in each size-class. Only size-classes with >10 individuals were analysed.

	t (metres)					n
	1	5	10	15	20	
D.dacrydioides						
≥5 cm dbh	U	.	C C C C C C C C C C C			160
Sd+S	C C C C C C C C C C C C C C C C C C C C					46
P.ferruginea						
≥5 cm dbh	. . . . .	. . . . .	. . . . .			14
Sd+S	C C C C C C C C C C C C C C C C C C C C					434
W.racemosa						
>20 cm dbh	. . . . .	. . . . .	. . . . .			100
≤20 cm, ≥5 cm dbh	C C . C C C C C C C C C C C C C C C C C					89

TABLE 8: Patterns of association for trees (by species and size-class) in stand K2 derived from the function $L_{12}(t)$. + and - denote significant ($P < 0.05$) positive and negative association for distances of t up to 5 m, . = no significant association. Sd+S = seedlings + saplings. Only size-classes with >10 individuals were analysed.

	D.dac Sd+S	*P.fer* ≥5 cm	*P.fer* Sd+S	*W.rac* >20 cm	*W.rac* ≤20 cm
D. dacrydioides, ≥5 cm dbh	–	.	+	+	.
D. dacrydioides, Sd+S		.	–	–	.
P. ferruginea, ≥5 cm dbh			+	.	.
P. ferruginea, Sd+S				+	+
W. racemosa, >20 cm dbh					–

MIXED CANOPY FOREST ESTABLISHED AFTER FLOODING

STAND F1

Stand structure and spatial distribution of tree ages

Stand F1 resembled an even-sized pole stand with dense *Dacrycarpus dacrydioides* and *Dacrydium cupressinum* 25 - 30 m tall forming the upper canopy (Table 1). *Weinmannia racemosa* dominated the lower canopy tier, occasionally reaching into the upper canopy. Canopy height was relatively uniform and the podocarp trees had narrow, pyramidal crowns.

The age structures for *Dacrycarpus dacrydioides* and *Dacrydium cupressinum* were determined by systematically coring samples of 70 and 78 trees respectively. Thirteen of the 18 *Prumnopitys ferruginea* ≥5 cm dbh were cored.

Size and age-class distributions of the four canopy species in stand F1 showed discontinuous patterns of recruitment (Fig 12). Normally distributed age-class distributions for *Dacrydium cupressinum*, *Dacrycarpus dacrydioides*, and *Prumnopitys ferruginea* suggested these three species established contemporaneously after catastrophic disturbance 200 - 250 years ago. The oldest *D. cupressinum*, *D. dacrydioides*, and *P. ferruginea* trees aged were 227, 226, and 238 years respectively. Over 95% of all aged podocarps were 100 - 250 years old. Little recruitment into the canopy had occurred in the last 100 years (Fig 12b,d,f). There were no *D. dacrydioides* seedlings or saplings growing beneath the canopy and only one *D. cupressinum* and nine *P. ferruginea*.

Dead standing *D. dacrydioides* were common in the smaller size-classes and may reflect thinning caused by density dependent mortality (Fig 12g). There were eight dead standing *D. cupressinum* and no dead standing *P. ferruginea* trees.

FIGURE 12: Size- and age-class frequency distributions for the main species in stand F1. n = number of trees. Size classes are: Sd = seedlings (≥0.5 m but <1.3 m tall); S = saplings (≥1.3 m tall but <5 cm dbh); 1 = 5 - 14.5 cm dbh; 2 = 15 - 24.5 cm dbh; 3 = 25 - 34.5 cm dbh etc.

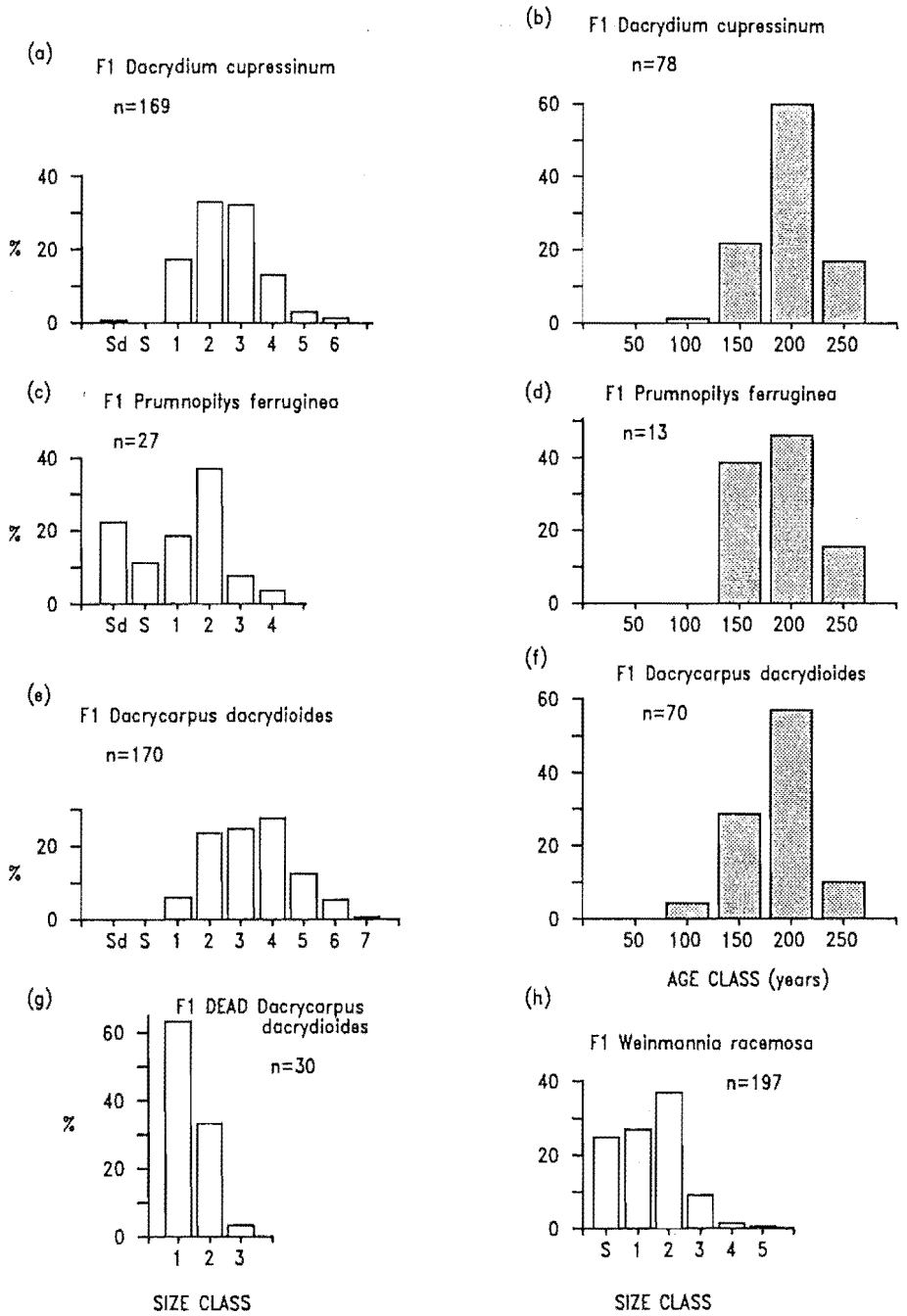
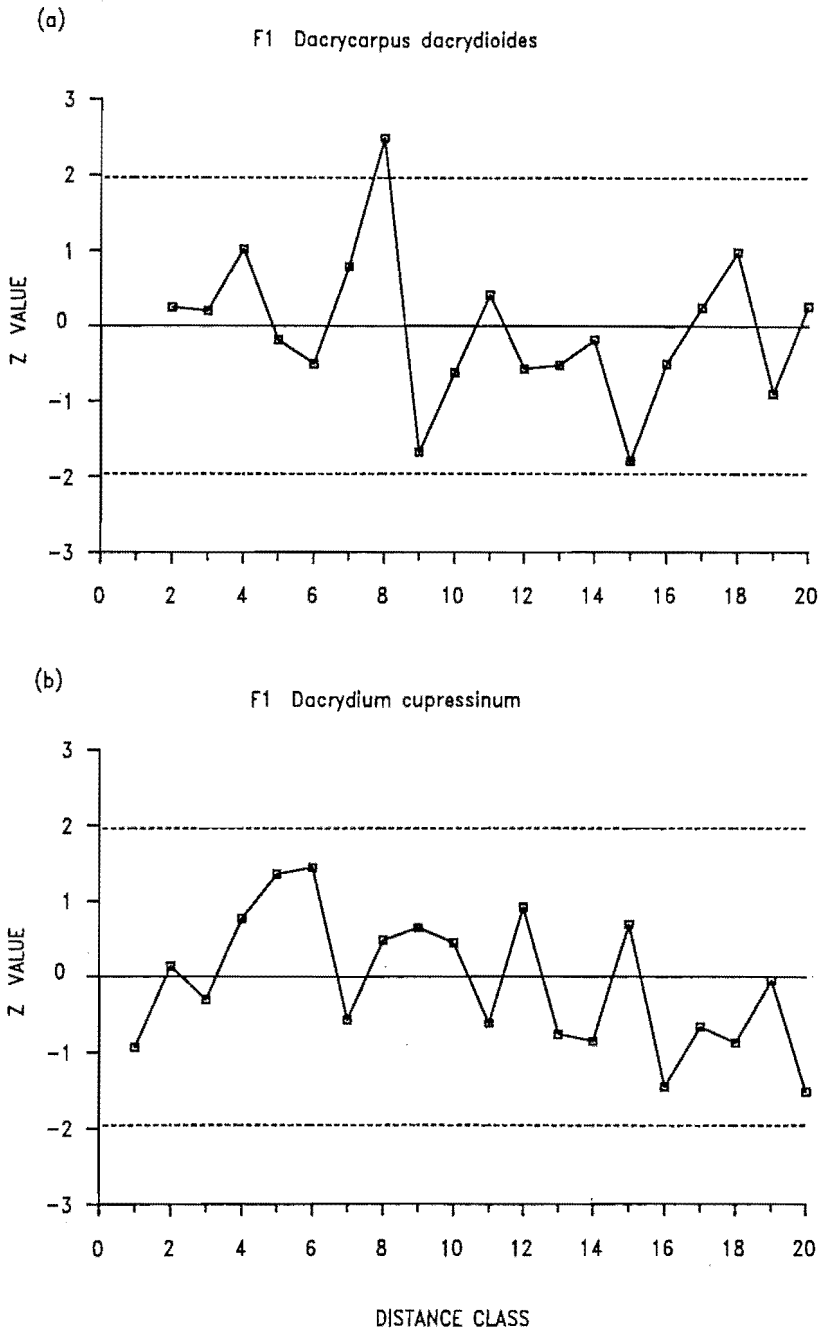


FIGURE 13: Spatial correlograms of (a) *Dacrycarpus dacrydioides* and (b) *Dacrydium cupressinum* tree ages in stand F1. Each distance class is a 3 m interval. Dotted lines indicate the 0.05 significance levels.



Correlograms of tree age for *D. dacrydioides* and *D. cupressinum* (Fig 13a,b) were not globally significant at the $\alpha = 0.05$ level. No spatial structure was evident from the shape of either correlogram suggesting that tree ages were randomly distributed among the given locations. The stand may have originated as a single cohort as there was no evidence of patchiness associated with establishment in more than one disturbance opening. However, small groups of even-aged trees may have been undetected because a systematic sample of trees were cored and most of the trees aged were not adjacent neighbours. There were too few *P. ferruginea* in the plot to construct a correlogram.

Weinmannia racemosa occurred in all size-classes from saplings to 45 cm dbh suggesting that it was successfully regenerating beneath the existing canopy (Fig 12h). However, the size-class distribution showed a discontinuous pattern of recruitment with a peak in the 15 - 24.5 cm dbh class. The regression between size and age for *W. racemosa* in F1 (Table 2) gave an age of 125 years for a 25 cm dbh tree which suggested that the majority of *W. racemosa* established after the majority of podocarp trees.

Regeneration patterns

Over 80% of trees established on elevated sites in stand F1 (Table 9). The majority of *Dacrycarpus dacrydioides* established on, or <0.5 m above, the ground and no trees established at a height of >1 m. This pattern of establishment was significantly different from the other three species (two-tailed Kolmogorov-Smirnov test, $P < 0.001$), in which ≥50% of trees established >0.5 m above the ground.

The three podocarp species differed in their growth rates (Table 2). Mean ring width of the cored *D. dacrydioides* trees (0.96 ± 0.27 mm) was significantly greater than *D. cupressinum* (0.73 ± 0.23 mm) which in turn was significantly greater than *P. ferruginea* (0.60 ± 0.17 mm), (t-test, $P < 0.05$). The distribution of trees in vertical height classes indicated a similar pattern in height growth (Table 1). Slower growing *P. ferruginea* trees

TABLE 9: Percentage of trees (by species and size-class) in establishment site and overhead cover classes for stand F1. L = level, E1 = elevated <0.5 m, E2 = elevated 0.5-1 m, E3 = elevated >1 m; C = closed, I = intermediate, O = open. Sd+S = seedlings + saplings. n = number of trees measured. Only size-classes with >5 individuals are included.

	Establishment site				Overhead cover			
	L	E1	E2	E3	C	I	O	n
D.dacrydioides								
≥5 cm dbh	36	45	19	0	3	9	88	170
D.cupressinum								
≥5 cm dbh	4	46	38	12	26	11	63	168
P.ferruginea								
≥5 cm dbh	6	33	55	6	66	17	17	18
Sd+S	11	78	11	0	100	0	0	9
W.racemosa								
≥5 cm dbh	7	32	37	24	28	27	45	148

were mainly in the lower main canopy or subcanopy tiers. The majority of *D. dacrydioides* were in the upper main canopy while *D. cupressinum* occurred intermediate between the two. The overtopping of slower growing trees was reflected in differences in the proportion of trees of each species in different overhead cover classes (Table 9).

The numbers of dead standing trees, relative abundances in different height tiers, and frequency occurrences in overhead cover classes suggested differences in the relative shade tolerance of the three podocarp species. The scarcity of *D. dacrydioides* trees in the lower canopy tiers and closed overhead cover class, and the abundance of dead standing trees in the smaller size-classes (Fig 12g) suggested that *D. dacrydioides* was unable to tolerate the lower light levels experienced by trees in the lower canopy and subcanopy tiers. There were no dead standing *Prumnopitys ferruginea*, and *P. ferruginea* trees and scattered seedlings and saplings occurred predominantly under a closed canopy, suggesting it was relatively shade tolerant. There were eight dead standing *Dacrydium cupressinum* trees all 15 - 34.5 cm dbh. The number of dead trees and the distribution of *D. cupressinum* in height and overhead cover classes suggested it was intermediate between *D. dacrydioides* and *P. ferruginea* in shade tolerance.

The majority of *Weinmannia racemosa* established >100 years after the establishment of podocarp trees in the stand. They would therefore have grown beneath a developing podocarp canopy. The majority of *W. racemosa* were in the lower canopy or subcanopy tiers (Table 1). Despite this, over 70% of *W. racemosa* occurred in the open or intermediate cover class (Table 9) suggesting that recruitment of *W. racemosa* occurred predominantly in canopy openings.

Disturbance history

Soils in plot F1 were recent and formed on alluvial silt >1 m deep. The depth of alluvium and lack of soil development suggested that past flood disturbance initiated

establishment of the relatively even-aged stand of *D. dacrydioides*, *D. cupressinum*, and *P. ferruginea*. Elevated sites, consisting of large mounds, stumps, or old logs covered about 37% of the plot surface (Table 3) and trees had established on most of these. The flood event that initiated regeneration of the canopy trees apparently did not completely clear the site but left exposed debris that provided establishment sites for most of the trees in the plot.

Spatial Patterns

Dacrycarpus dacrydioides trees were randomly or uniformly distributed at distances up to 5 m (Table 10). Patterns of non-random mortality suggested that thinning had resulted in a change in the spatial dispersion of trees, from a clumped to a significantly uniform distribution at small distances (Fig 14).

Clumping of *D. cupressinum* and *W. racemosa* at small distances (Table 10) can be attributed to establishment on elevated sites and may also reflect establishment of *W. racemosa* in small canopy openings. Clumping of *D. dacrydioides*, *D. cupressinum*, and *W. racemosa* at distances >5 m probably reflects broad-scale patchiness in the distribution of suitable establishment sites throughout the plot.

Significant positive spatial association between *W. racemosa*, *D. cupressinum*, and *P. ferruginea* (Table 11) reflects their preferences for similar establishment sites. These three species combined were negatively associated with *D. dacrydioides* trees which established on different sites.

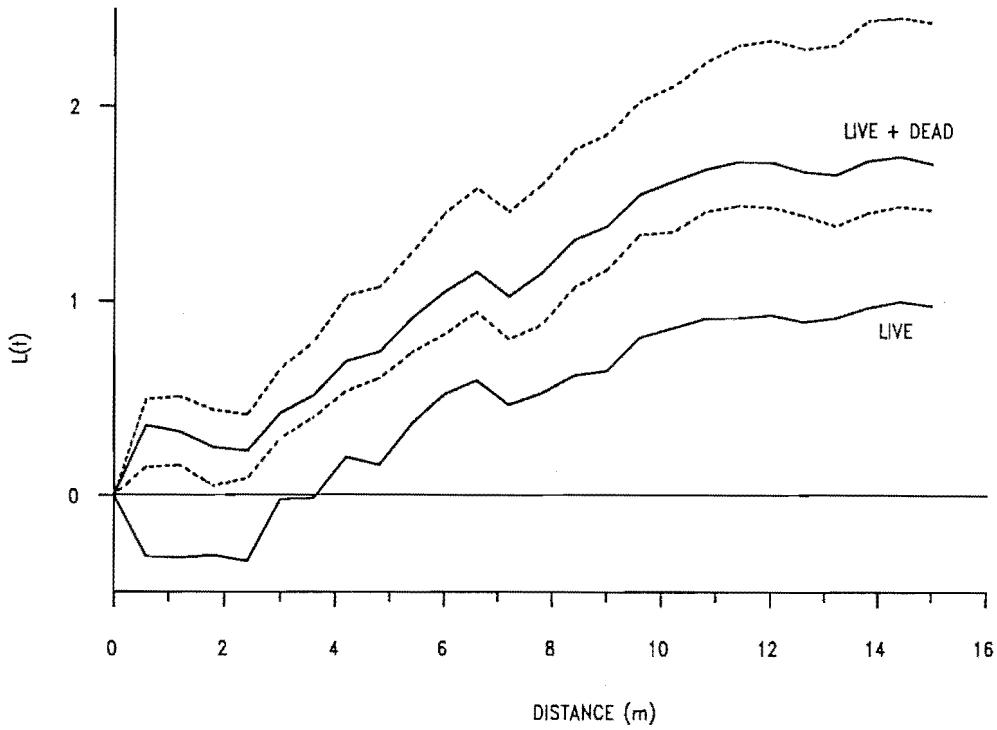
TABLE 10: Patterns of spatial dispersion for trees (by species and size-class) in stand F1. Letters indicate significant ($P < 0.05$) deviation from a random distribution at distance t based on values of the function $L(t)$; U = uniform distribution, C = clumped distribution, . = random. Sd+S = seedlings + saplings, n = number of individuals in each size-class. Only size-classes with >10 individuals were analysed.

	t (metres)					n
	1	5	10	15	20	
D.dacrydioides						
≥5 cm dbh	. U . . .	C C C C C C C C C C C C C C C C C C C C				170
D.cupressinum						
≥5 cm dbh	. .	C C C C C C C C C C C C C C C C C C C C				168
P.ferruginea						
≥5 cm dbh	. . . . .	. . . . .	. . . . .	. . . . .	. . . . .	18
W.racemosa						
≥5 cm dbh	C C C C C C C C C C C C C C C C C C C C					148

TABLE 11: Patterns of association for trees (by species and size-class) in stand F1 derived from the function $L_{12}(t)$. + and - denote significant ($P < 0.05$) positive and negative association for distances of t up to 5 m, . = no significant association. Sd+S = seedlings + saplings; Comb. = all trees of *Dacrydium*, *Prumnopitys*, and *Weinmannia* ≥5 cm dbh; NA = not applicable. Only size-classes with >10 individuals were analysed.

	D.cup ≥5 cm	*P.fer* ≥5 cm	*W.rac* ≥5 cm	Comb.
D.dacrydioides, ≥5 cm dbh	.	.	.	–
D.cupressinum, ≥5 cm dbh		.	+	NA
P.ferruginea, ≥5 cm dbh			+	NA

FIGURE 14: The function *L(t)* for *Dacrycarpus dacrydioides* ≥5 cm dbh in stand F1, with the post-mortality pattern (live stems) tested against the null hypothesis of random mortality in the pre-mortality distribution (live + dead stems). 95% confidence envelopes (dotted lines) show the pattern expected after random mortality.



STAND F2

Stand Structure and spatial distribution of tree ages

Scattered, large-crowned *Dacrycarpus dacrydioides* and *Dacrydium cupressinum* 35 - 40 m tall, together with smaller diameter, lighter-crowned trees formed the upper canopy tier in stand F2 (Table 1). Trees of *Weinmannia racemosa*, *Prumnopitys ferruginea*, *Dacrydium cupressinum*, and *Dacrycarpus dacrydioides* were present in the lower canopy with *W. racemosa* and *P. ferruginea* dominant in the subcanopy.

Two distinct cohorts, the older c. 350 - 550 years and the younger c. 150 - 250 years, were evident in the age distributions of *Dacrycarpus dacrydioides* and *Dacrydium cupressinum* in stand F2 (Fig 15b,d).

The spatial correlogram of *D. dacrydioides* tree age (Fig 16a) was globally significant at the $\alpha = 0.05$ level and the shape of the correlogram indicated patchiness in the distribution of tree ages. Significant positive autocorrelation in distance classes 2 - 4 (>3 - 12 m) was attributed to the association of trees of similar age within patches. Differences in age between patches was reflected in significant negative autocorrelation in distance classes ≥14 (>39 m).

Clusters of points, representing patches of trees, were evident in the ordination diagram (Fig 16b). These clusters corresponded to the two cohorts evident in the *D. dacrydioides* age distribution. The older cohort of trees (>250 years old) consisted of two patches (clusters 1 and 2 in Fig 16b). The largest patch was in the northern third of the plot and the second patch consisted of two outlier trees in the south-western corner of the plot (Fig 17a). The younger cohort of *D. dacrydioides* trees (150 - 242 years old) was identified as a third patch (cluster 3 in Fig 16b) which occurred in the central region of the plot (Fig 17b).

FIGURE 15: Size- and age-class frequency distributions for the main species in stand F2. n = number of trees. Size classes are: Sd = seedlings (≥0.5 m but <1.3 m tall); S = saplings (≥1.3 m tall but <5 cm dbh); 1 = 5 - 14.5 cm dbh; 2 = 15 - 24.5 cm dbh; 3 = 25 - 34.5 cm dbh etc.

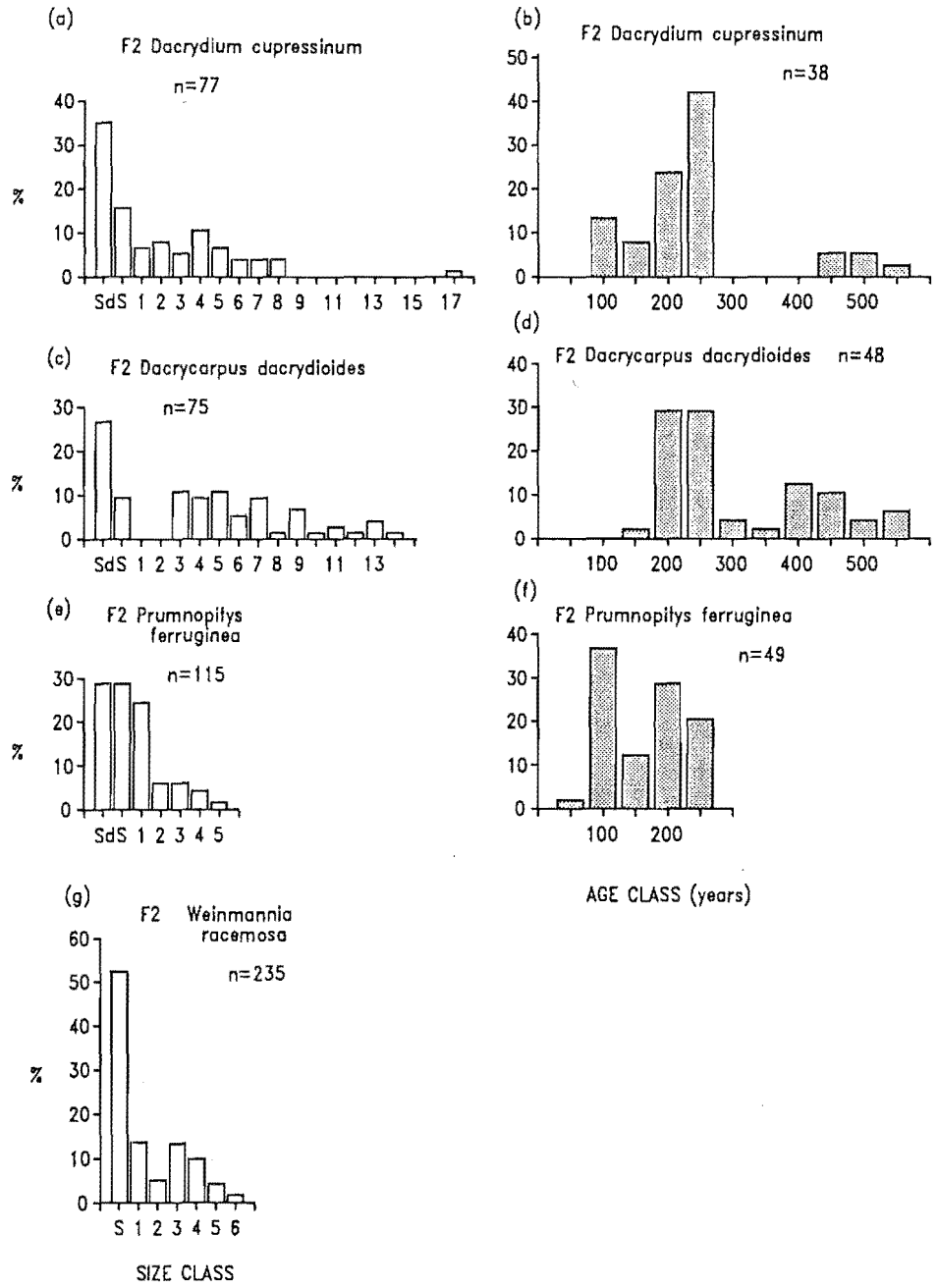


FIGURE 16: (a) Spatial correlogram of *Dacrycarpus dacrydioides* tree ages in stand F2. Each distance class is a 3 m interval. Dotted lines indicate the 0.05 significance levels. (b) Scatter diagram obtained from an ordination of the association measure c_{ij}, reflecting tree age differences and spatial proximity, for aged *Dacrycarpus dacrydioides* in stand F2. The circled groups are clusters of trees identified as patches (see text).

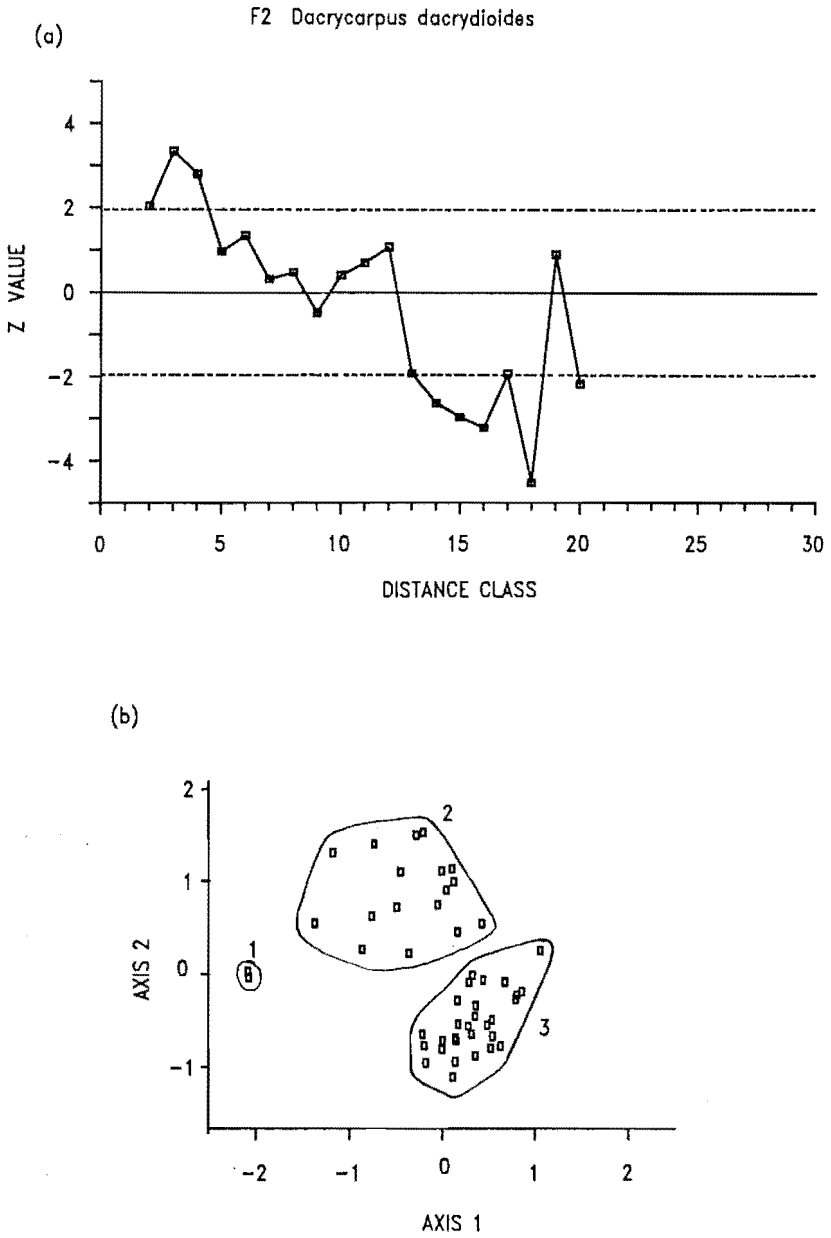
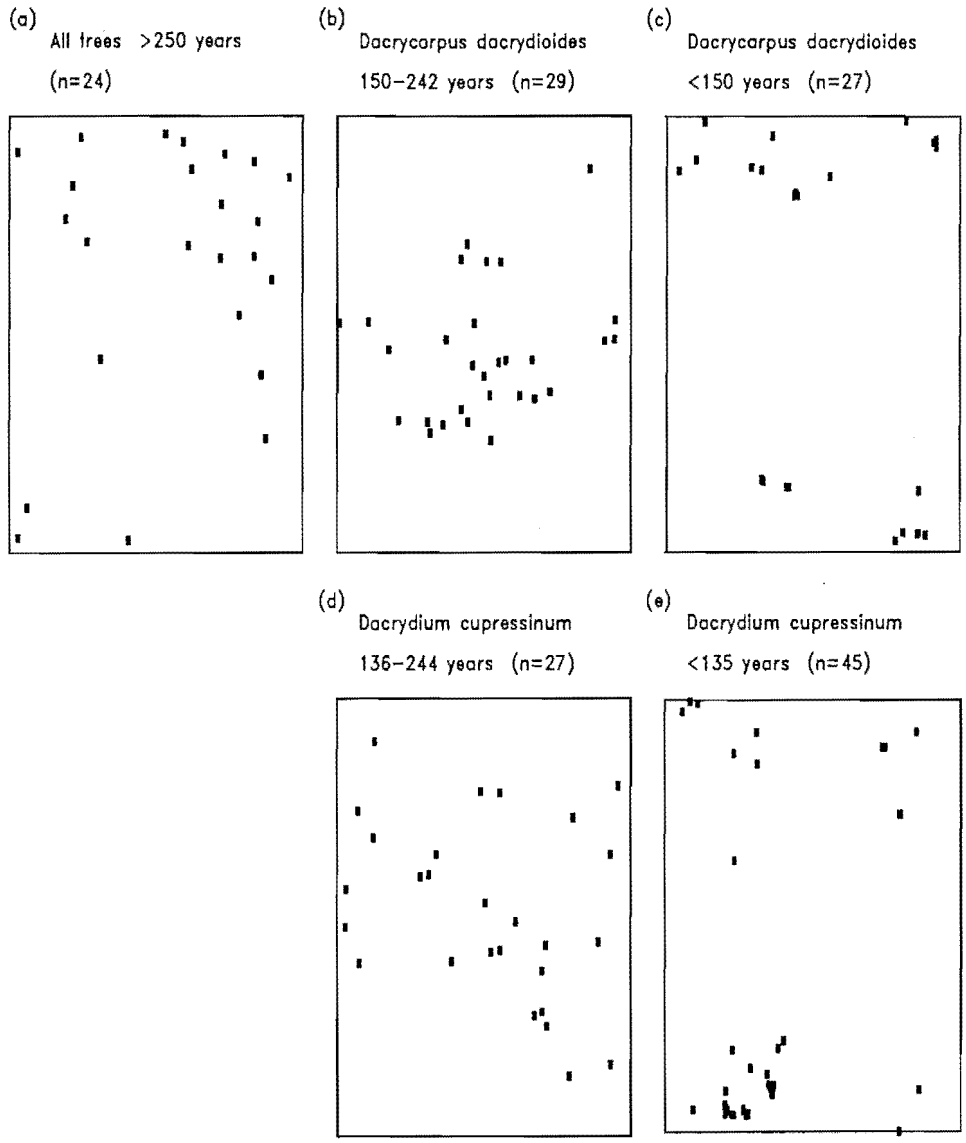


FIGURE 17: Stem maps of species age-groups in stand F2. n = number of stems.



Gaps in the size and age-class distributions indicated that regeneration of *D. dacrydioides* occurred sporadically. No recruitment into the canopy had occurred in the last 150 years (Fig 15c,d). The spatial distribution of *D. dacrydioides* <150 years old (the seedlings and saplings) was patchy with establishment restricted to the northern and southern thirds of the plot (Fig 17c).

The correlogram of *Dacrydium cupressinum* tree age (Fig 18a) was globally significant at the $\alpha = 0.05$ level. The small number of trees meant that distance classes 1 - 4 and 24 -30 contained fewer than 20 pairs of point locations and so were not interpreted. Tree age was significantly negatively autocorrelated in distance class 23, indicating that trees >66 -69 m apart tended to be of different age, and suggesting broad-scale patchiness in the distribution of tree ages.

Clusters of points, representing patches of trees, were evident in the ordination diagram (Fig 18b). These clusters corresponded to the cohorts evident in the *Dacrydium cupressinum* age distribution. The majority of trees comprising the older cohort (>250 years; cluster 1 in Fig 18b) occurred in the northern third of the plot, with a single tree (cluster 2 in Fig 18b) at the southern end (Fig 17a). Trees in the younger cohort (136 - 244 years; cluster 3 in Fig 18b) were identified as a second patch occurring in the central region of the plot (Fig 17d). Aged *D. cupressinum* trees <136 years old were recognised as a third patch (cluster 4 in Fig 18b). Mapping aged trees <136 years old, along with seedlings and saplings of *D. cupressinum* (all of which were likely to be <136 years old), showed that recent establishment was confined to the northern and southern thirds of the plot (Fig 17e). *D. cupressinum* occurred in the range of smaller size-classes (Fig 15a) suggesting that it was successfully regenerating beneath the existing canopy.

The size-class distribution of *Prumnopitys ferruginea* resembled a reverse J-shaped curve which, apart from a lack of seedlings, suggested a pattern of continuous

FIGURE 18: (a) Spatial correlogram of *Dacrydium cupressinum* tree ages in stand F2. Each distance class is a 3 m interval. Dotted lines indicate the 0.05 significance levels. (b) Scatter diagram obtained from an ordination of the association measure c_{ij}, reflecting tree age differences and spatial proximity, for aged *Dacrydium cupressinum* in stand F2. The circled groups are clusters of trees identified as patches (see text).

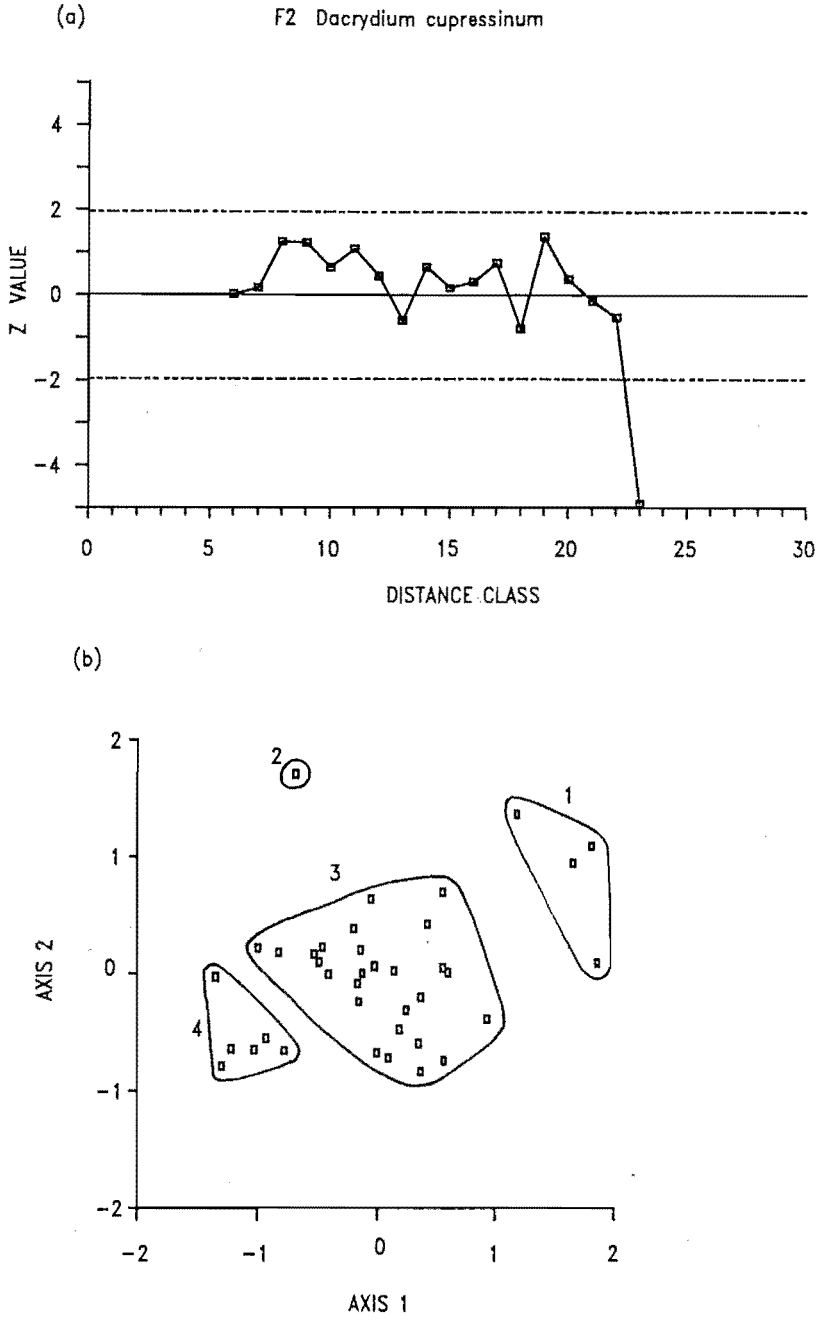


FIGURE 19: (a) Spatial correlogram of *Prumnopitys ferruginea* tree ages in stand F2. Each distance class is a 3 m interval. Dotted lines indicate the 0.05 significance levels. (b) Scatter diagram obtained from an ordination of the association measure c_{ij}, reflecting tree age differences and spatial proximity, for aged *Prumnopitys ferruginea* in stand F2. The circled groups are clusters of trees identified as patches (see text).

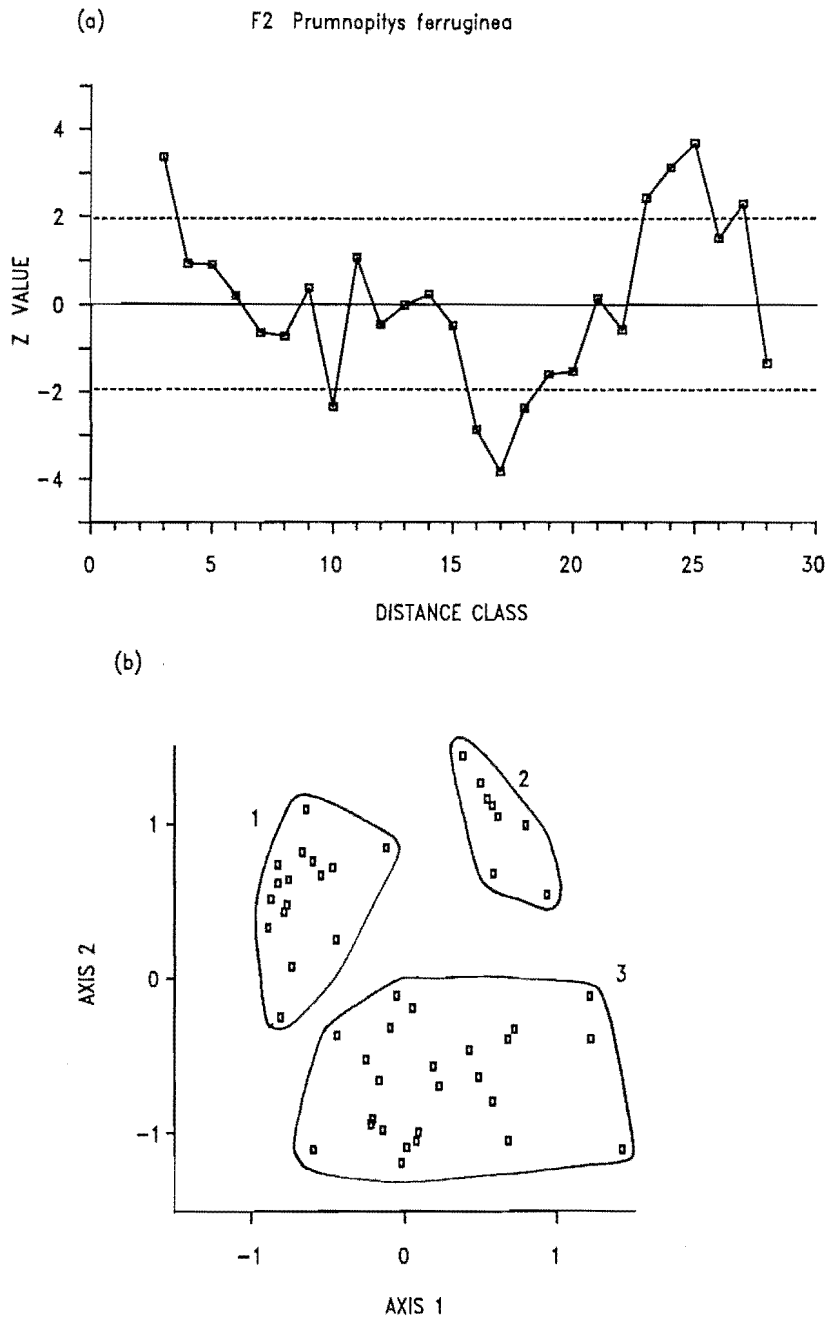
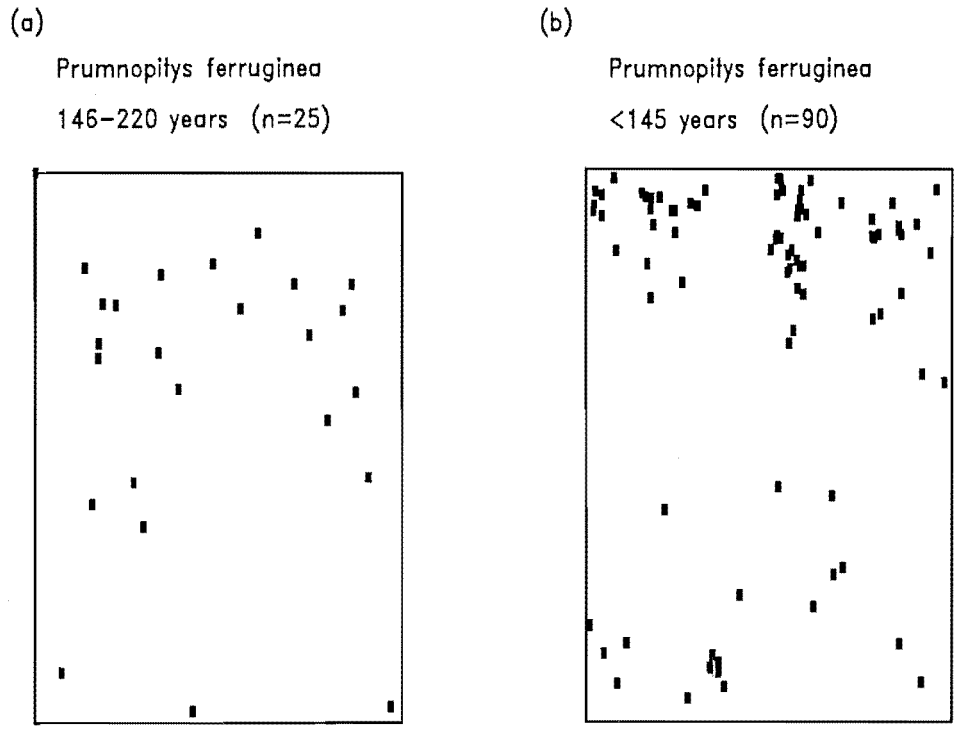


FIGURE 20: Stem maps of *Prumnopitys ferruginea* age-groups in stand F2. n = number of stems.



regeneration (Fig 15e). The age-class distribution (Fig 15f), however, revealed a discontinuous pattern of recruitment. An abundance of individuals 150 - 250 years old indicated a period of increased establishment contemporaneous with cohorts of *D. dacrydioides* and *D. cupressinum*.

The spatial correlogram of *P. ferruginea* tree age (Fig 19a) was globally significant at the $\alpha = 0.05$ level. The alternating significant positive and negative values indicated patchiness in the spatial distribution of tree ages. Significant positive autocorrelation at small and large distances reflected the association of trees of similar age within patches, and the distance between patches of similar age. Significant negative autocorrelation at intermediate distances corresponded to the distance between patches of different age.

Two fairly distinct clusters of points were evident in the ordination diagram (clusters 1 and 2 in Fig 19b). These two clusters were *P. ferruginea* trees <146 years old. Mapping these trees along with seedlings and saplings of *P. ferruginea* (all of which are likely to be <146 years old) revealed two distinct patches occurring in the northern and southern thirds of the plot (Fig 20b). The remainder of trees in the ordination diagram (cluster 3 in Fig 19b) were *P. ferruginea* 146 - 220 years old. This older group of trees occurred more towards the centre of the plot than the two patches of trees <146 years old (Fig 20a,b).

In the spatial correlogram, significant negative autocorrelation in distance classes 10 (>27 -30 m) and 16 - 18 (>45 - 54 m) (Fig 19a) reflected the difference in age between the two younger patches (<146 years old) at the northern and southern ends of the plot, and the older patch (146 - 220 years old) in the more central region. The presence of two similarly-aged patches at opposite ends of the plot was reflected in significant positive autocorrelation in distance classes 23 - 25 (>66 - 75 m) and 27 (>78 - 81 m).

P. ferruginea trees were common in the range of smaller age and size-classes (Fig

15e,f) which suggested that *P. ferruginea* was successfully regenerating in stand F2.

The size distribution of *Weinmannia racemosa* (Fig 15g) suggested a pattern of recruitment similar to that of *P. ferruginea*. The large number of saplings and the occurrence of trees in all size-classes <65 cm dbh suggested that *W. racemosa* was successfully regenerating in the stand. An abundance of individuals 35 - 54.5 cm diameter indicated a period of increased establishment. The regression between size and age for *W. racemosa* in stand F2 (Table 2) gave an age of 264 years for a 55 cm diameter tree indicating the pulse of recruitment was approximately synchronous with those evident in the podocarp age-class distributions.

Regeneration Patterns

The majority of *Dacrydium cupressinum*, *Prumnopitys ferruginea*, and *Weinmannia racemosa* ≥5 cm dbh established on elevated sites in stand F2 (Table 12). The establishment pattern of *Dacrycarpus dacrydioides* was significantly different from the other species (two-tailed Kolmogorov-Smirnov test, $P < 0.001$). Eighty eight percent of *D. dacrydioides* ≥5 cm dbh established on the ground and only 12% on elevated sites, all <0.5 m above the ground. Patterns of seedling and sapling establishment were similar to the establishment patterns of trees ≥5 cm dbh for *D. dacrydioides*. However, a greater proportion of *D. cupressinum* and *P. ferruginea* seedlings and saplings had established on higher elevated sites.

The majority of *D. dacrydioides* and *D. cupressinum* occurred in the open overhead cover class (Table 12) reflecting their dominance in the upper canopy tiers (Table 1). In contrast the majority of *P. ferruginea* occurred in the lower canopy or subcanopy tiers and in the closed or intermediate overhead cover class. While *W. racemosa* also occurred in the lower canopy or subcanopy tiers, 71% of trees were in the open cover class. This reflected the importance of canopy openings for successful *W.*

TABLE 12: Percentage of trees (by species and size-class) in establishment site and overhead cover classes in stand F2. L = level, E1 = elevated >0.5 m, E2 = elevated 0.5 - 1 m, E3 = elevated >1 m; C = closed, I = intermediate, O = open. Sd+S = seedlings + saplings. n = number of trees measured. Only size-classes with >5 individuals are included.

	Establishment site				Overhead cover			
	L	E1	E2	E3	C	I	O	n
D.dacrydioides								
≥5cm dbh	88	6	6	0	0	2	98	48
Sd+S	78	22	0	0	82	11	7	27
D.cupressinum								
≥5cm dbh	21	26	37	16	5	8	87	38
Sd+S	3	5	13	79	44	41	15	39
P.ferruginea								
≥5cm dbh	4	59	21	16	39	12	49	49
Sd+S	3	32	35	30	68	21	11	66
W.racemosa								
≥5cm dbh	12	33	25	30	10	19	71	112

racemosa regeneration.

Disturbance history

The temporal patterns of tree establishment indicated that two major disturbance events initiated recruitment of the majority of trees in the plot. The older cohort of *D. dacrydioides* and *D. cupressinum* was dominated by trees 350 - 500 years old. The age of the oldest tree cored (503 years) indicated that this cohort originated at about the same time as the trees in stand K2 and the oldest cohort in stand K1.

A pulse of recruitment c. 150 - 250 years ago, evident in the age distributions of all three podocarp species and in the size distribution of *W. racemosa*, indicated a second disturbance event. The ages of the oldest *D. dacrydioides*, *D. cupressinum*, and *P. ferruginea* trees in this cohort (242, 244 and 220 years respectively) indicated that the cohort originated at about the same time as the cohort in stand F1.

Stand F2 was located at the base of the front range of the Southern Alps. Soils in the plot were recent and formed on alluvial silt and gravel up to 1 m deep. The depth of alluvium and lack of soil development suggested that flood disturbance formed openings for the establishment of the younger cohort of trees and probably also initiated establishment of the older cohort. Logs buried in silt and gravel were found under uprooted trees in and near the plot. These buried logs were probably remnants of the original forest destroyed by flood disturbance.

The patchy spatial distribution of tree ages suggested that the disturbance event that initiated the younger cohort of trees (c. 150 - 250 years old) varied in its effect throughout the plot. Older trees that survived the flood were confined to the northern and southern thirds of the plot. Trees that established in response to the disturbance occurred mainly in the central region. The flood appeared to have channelled through the middle

of the plot and destroyed most of the original forest in a strip through the central region, forming a large opening in which trees subsequently established.

Spatial patterns

The spatial distribution of trees in size and age-classes reflected the response of species to intermittent disturbance (Table 13). Trees in all age-classes were significantly clumped at distances up to 20 m apart reflecting the patchy distribution of age-classes in the plot (Fig 17,20). Differences in the scale at which trees were clumped reflected the different response of species to the same disturbance event. *Dacrycarpus dacrydioides* 150 - 242 years old were clumped at distances >4 m with establishment confined to a relatively compact patch in the middle of the plot (Fig 17b). In contrast *D. cupressinum* 136 - 244 years old and *P. ferruginea* 146 - 220 years old were clumped at a distance of 10 m or greater but were mostly randomly dispersed at distances up to 20 m, reflecting a more dispersed pattern of establishment in larger patches.

The youngest age-classes of all three podocarp species were clumped at all distances up to 20 m. At small scales clumping can be attributed to the patchiness of suitable establishment sites. At larger scales all three species had a similar patchy distribution and were largely confined to the northern and southern ends of the plot. Clumping of large (>30 cm dbh) and smaller (≤30 cm dbh) *Weinmannia racemosa* at distances up to 5 m can be attributed to establishment on elevated sites and in canopy openings.

The different response of species to the flood disturbance that initiated the younger cohort of trees (c. 150 - 250 years old) was evident in the patterns of spatial association among size and age-classes (Table 14). *Dacrycarpus dacrydioides* 150 - 242 years old established in the central region of the plot and were negatively associated with trees >250 years old that survived the flood event. *Dacrydium cupressinum* 136 - 244 years old also

established in the central region of the plot and were positively associated with *D. dacrydioides* 150 - 242 years old. However, *D. cupressinum* 136 - 244 years old were spatially independent of trees >250 years old. This suggests that establishment of *D. cupressinum* was not confined to openings away from the remnant canopy.

Prumnopitys ferruginea 146 - 220 years established among the trees that survived the disturbance event and were positively associated with trees >250 years old. Negative association with *D. dacrydioides* 150 - 242 years old suggested that establishment of *P. ferruginea* did not occur in openings away from the surviving canopy.

Weinmannia racemosa >30 cm dbh, most of which established in a pulse of recruitment following the flood disturbance, had a similar spatial distribution to *P. ferruginea*. Positive association with trees >250 years old indicated *W. racemosa* established among the surviving canopy trees. Negative association with *D. dacrydioides* 150 - 242 years old, and *D. cupressinum* 136 - 244 years old suggested *W. racemosa* did not establish in openings away from the remnant canopy.

P. ferruginea <146 years old and *W. racemosa* ≤30 cm dbh were both positively associated with trees >250 years old. Recent regeneration of these two species had occurred beneath the canopy of older cohort trees. *D. dacrydioides* <150 years old and *D. cupressinum* <136 years old occurred in the same region of the plot as trees >250 years old (Fig 17) but were not significantly associated. Recent establishment of *D. dacrydioides* and *D. cupressinum* had not occurred directly beneath the older cohort trees.

TABLE 13: Patterns of spatial dispersion for trees (by species and age/size-class) in stand F2. Letters indicate significant ($P < 0.05$) deviation from a random distribution at distance t based on values of the function $L(t)$; U = uniform distribution, C = clumped distribution, . = random. Sd+S = seedlings + saplings, n = number of individuals in each age/size-class. Only age/size-classes with >10 individuals were analysed.

	t (metres) 1 5 10 15 20	n
D.dacrydioides		
>250 yrs	. . . . . C C C C	19
150-242 yrs	. . . C C C C C C C C C C C C C C C C C	29
<150 yrs	C C C C C C C C C C C C C C C C C C C C	27
D.cupressinum		
>250 yrs	too few for analysis	5
136-244 yrs	. . . . . C	27
<136 yrs	C C C C C C C C C C C C C C C C C C C C	45
P.ferruginea		
146-220 yrs	. . . . . C	25
<146 yrs	C C C C C C C C C C C C C C C C C C C C	90
W.racemosa		
>30cm dbh	C . C C C	48
≤30cm dbh	C C . C C C C C C C C . C . C C C C C	64

TABLE 14: Patterns of association for trees (by species and age/size-class) in stand F2 derived from the function $L_{12}(t)$. + and - denote significant ($P < 0.05$) positive and negative association for distances of t up to 15 m, . = no significant association. Only age/size-classes with >10 individuals were analysed.

	D.dac 150-242	*D.dac* <150	*D.cup* 136-244	*D.cup* <136	*P.fer* 146-220	*P.fer* <146	*W.rac* >30cm	*W.rac* ≤30cm
All trees								
>250 yrs	_	.	.	.	+	+	+	+
D.dacrydiodes								
>250 yrs	.	.	.	.	+	.	+	.
150-242 yrs		.	+	.	.	_	_	.
<150 yrs			.	.	.	+	.	+
D.cupressinum								
136-244 yrs				_	.	.	_	+
<136 yrs					.	+	+	.
P.ferruginea								
146-220 yrs						.	.	+
<146 yrs							+	+
W.racemosa								
>30cm dbh								+

MIXED CANOPY FOREST ESTABLISHED AFTER WIND DISTURBANCE

Plots M1 and M2 were located about 100 m from each other. In both plots large podocarps (>30 m tall), predominantly *Dacrydium cupressinum*, were emergent over lower canopy tiers 10 - 20 m tall. These lower tiers were dominated by *Dacrycarpus dacrydioides* in stand M1, and codominated by all four species in stand M2 (Table 1). Drainage patterns were different in the two stands. Most of plot M1 was poorly drained and 32% of the ground surface was covered by large, wet depressions (Table 3) that were filled with water for most of the year. Plot M2 was on a better drained site with only 6% of the ground surface covered by depressions. Drainage patterns varied within stands and wet depressions were distributed patchily throughout.

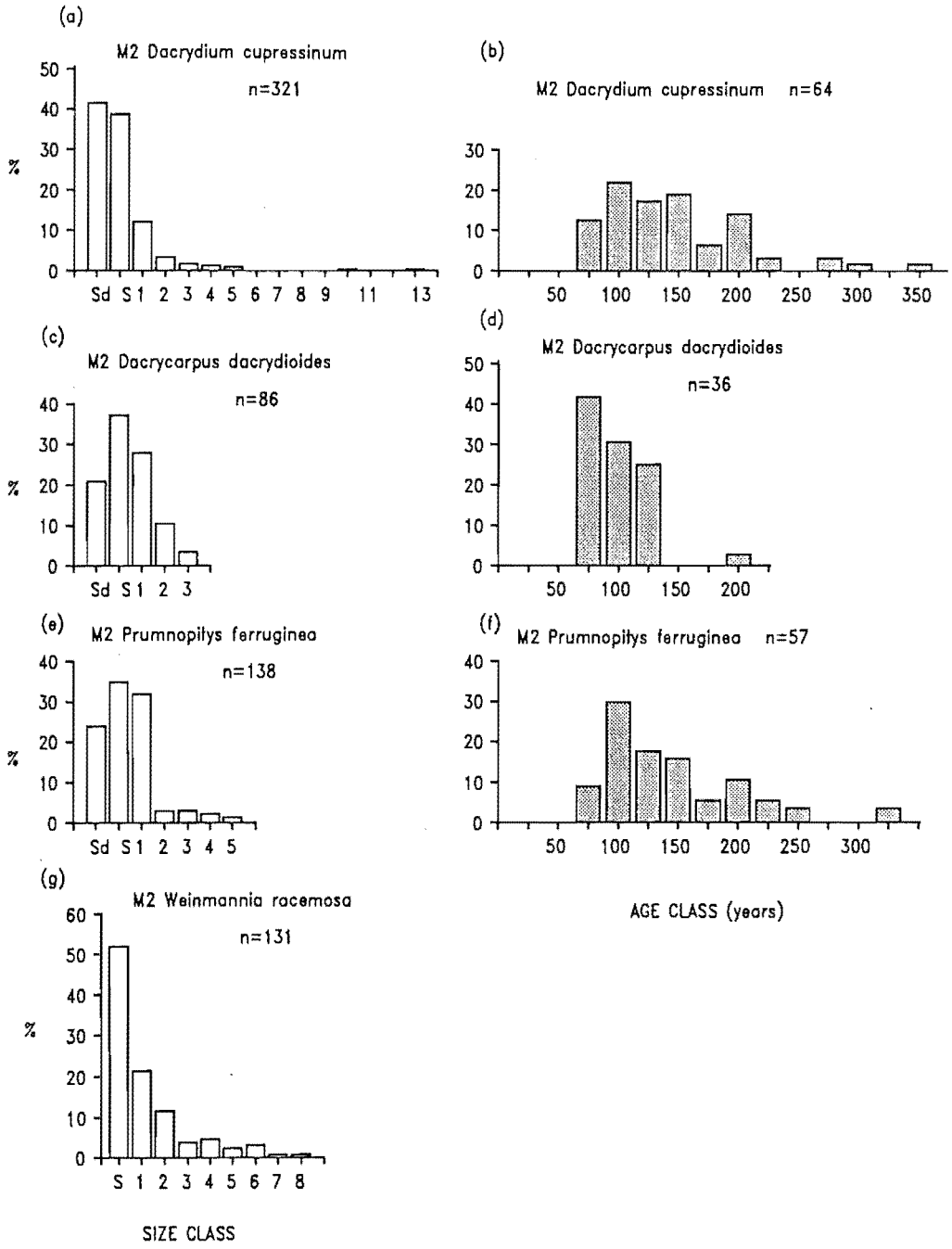
STAND M2

Stand structure and spatial distribution of tree ages

The size distributions of all four species in stand M2 were similar with >70% of trees <15 cm dbh (Fig 21). The size distributions of *D. cupressinum*, *P. ferruginea*, and *W. racemosa* resembled reverse J-shaped curves. This could reflect a relatively continuous pattern of recruitment and constant diameter-specific mortality rates or alternatively, increased recruitment of individuals into smaller size-classes triggered by historical events (Parker 1986). There were only scattered podocarp trees >250 years old in the stand (Fig 21b,d,f). The lack of older individuals and the abundance of trees <250 years old suggested a recent upsurge in recruitment of *Dacrydium cupressinum*, *Dacrycarpus dacrydioides*, and *Prumnopitys ferruginea*.

There were two *Dacrydium cupressinum* trees >95 cm dbh in stand M2 (Fig 21a). These trees were too large to core and their ages were estimated at 289 and 326 years from the regression of age against diameter for the 54 smaller *D. cupressinum* trees cored

FIGURE 21: Size- and age-class frequency distributions for the main species in stand M2. n = number of trees. Size classes are: Sd = seedlings (≥0.5 m but <1.3 m tall); S = saplings (≥1.3 m tall but <5 cm dbh); 1 = 5 - 14.5 cm dbh; 2 = 15 - 24.5 cm dbh; 3 = 25 - 34.5 cm dbh etc.



in the plot (Table 2). The estimated ages of the two trees >95 cm dbh may be under-estimates of their true age as *D. cupressinum* trees of comparable size (81 -91 cm dbh) cored in stand F2 and neighbouring stand M1 ranged in age from 425 - 513 years.

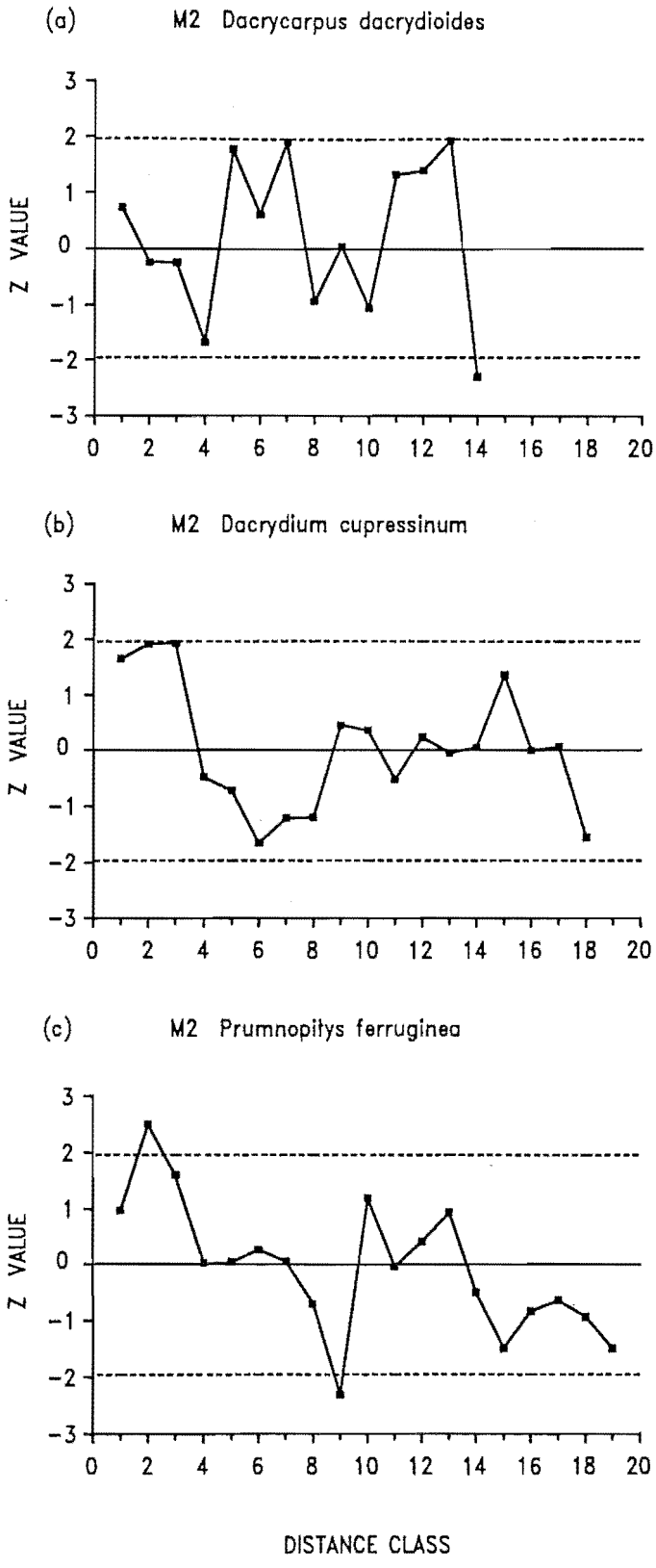
The remaining *Dacrydium cupressinum* trees were all <55 cm dbh and of these the oldest was 255 years. The age distribution showed recruitment of *D. cupressinum* occurred in all of the 25 year age-class intervals from 50 - 225 years with a slight pulse evident in the 175 - 200 year age-class. *D. cupressinum* seedlings and saplings were abundant in the plot.

The age-class distribution of *Prumnopitys ferruginea* was similar to *D. cupressinum*. There were two trees >300 years old with the remaining trees all <250 years old. *P. ferruginea* had successfully regenerated throughout the past 250 years; it occurred in all of the 25 year age-class intervals from 50 - 250 years. Periods of increased establishment were evident in the 175 - 200 and 75 - 100 year age-classes. *P. ferruginea* seedlings and saplings were common.

Dacrycarpus dacrydioides had the most discontinuous pattern of recruitment. There were no trees >200 years old in the plot and a single tree 188 years old had established during the period of increased *D. cupressinum* and *P. ferruginea* recruitment (175 - 200 year age-class). Increased recruitment of *D. dacrydioides* commenced about 125 years ago.

Weinmannia racemosa trees occurred in the range of size-classes up to 85 cm dbh, indicating a relatively continuous pattern of recruitment. Many of the larger *W. racemosa* in the stand had suffered past damage and had dead or broken stems, but had subsequently resprouted vegetatively.

FIGURE 22: Spatial correlograms of (a) *Dacrycarpus dacrydioides*, (b) *Dacrydium cupressinum* and (c) *Prumnopitys ferruginea* tree ages in stand M2. Each distance class is a 3 m interval. Dotted lines indicate the 0.05 significance levels.



Spatial correlograms of tree age for each of the three podocarp species (Fig 22) all failed to exceed the $\alpha = 0.05$ global significance level. The shape of the *D. dacrydioides* correlogram did not indicate a patch structure in the distribution of tree ages. However, while the *D. cupressinum* and *P. ferruginea* correlograms were not globally significant the shape of both correlograms suggested patchiness in the distribution of tree ages. Both correlograms showed positive autocorrelation in the first three distance classes indicating that trees of similar age tended to occur together. Negative troughs in subsequent distance classes suggested patches of different age.

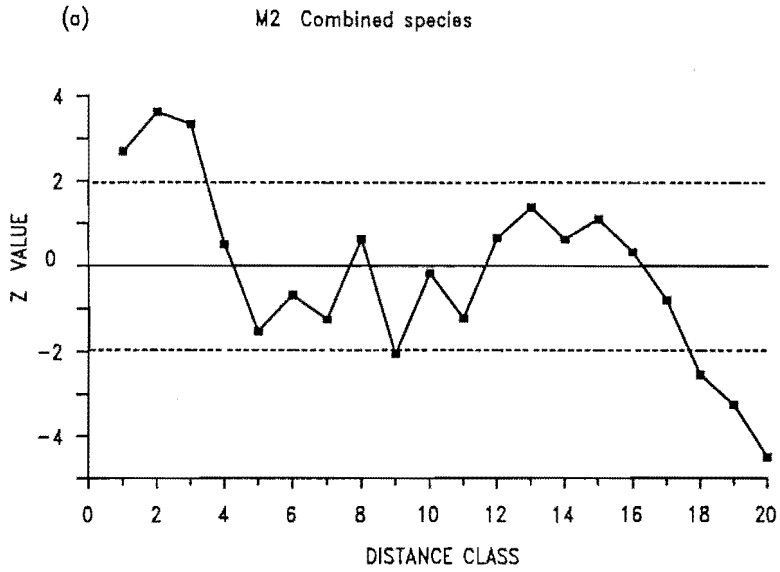
When tree ages of all three species were combined the resulting correlogram (Fig 23a) was globally significant at the $\alpha = 0.05$ level. Significant positive autocorrelation in distance classes 1 - 3 (0 - 9 m) indicated that trees of similar age occurred together in patches. Significant negative autocorrelation in distance classes 18 - 20 (>51 - 60 m) suggested there were patches of different-aged trees at opposite ends of the plot.

The cluster dendrogram and ordination diagram (Fig 23b) revealed a complex structure in the distribution of tree ages. Separate clusters of points, representing distinct patches, were not evident in the ordination diagram. However, small even-aged patches of trees could be identified as tight clumps of points in the ordination diagram.

Patterns in the distribution of different age-classes are illustrated in Fig 24. Trees in the same age-class tended to occur together in patches of varying size. These patches correspond to the small clusters evident in the ordination diagram. Furthermore, trees in the three different age-classes tended to occur in different parts of the plot. In some regions trees in the same age-class formed a distinct patch but in other areas of the plot age-classes spatially overlapped.

These patterns indicate that some recruitment occurred in relatively small, localised

FIGURE 23: (a) Spatial correlogram of all podocarp tree ages in stand M2. Each distance class is a 3 m interval. Dotted lines indicate the 0.05 significance levels. (b) Scatter diagram obtained from an ordination of the association measure c_{ij}, reflecting tree age differences and spatial proximity, for all aged podocarp trees in stand M2.



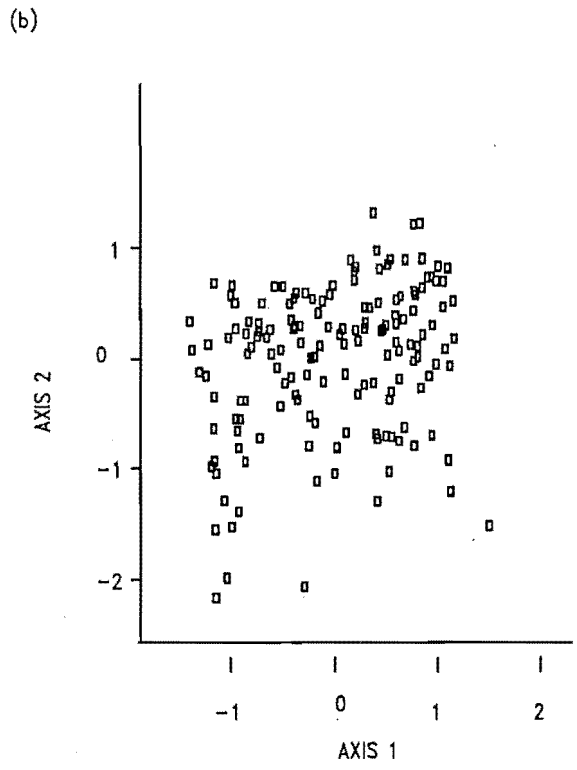


FIGURE 24: Stem maps of age-groups in stand M2. The symbols represent different species: ◊ = *Dacrycarpus dacrydioides*; ■ = *Dacrydium cupressinum*; + = *Prumnopitys ferruginea*.

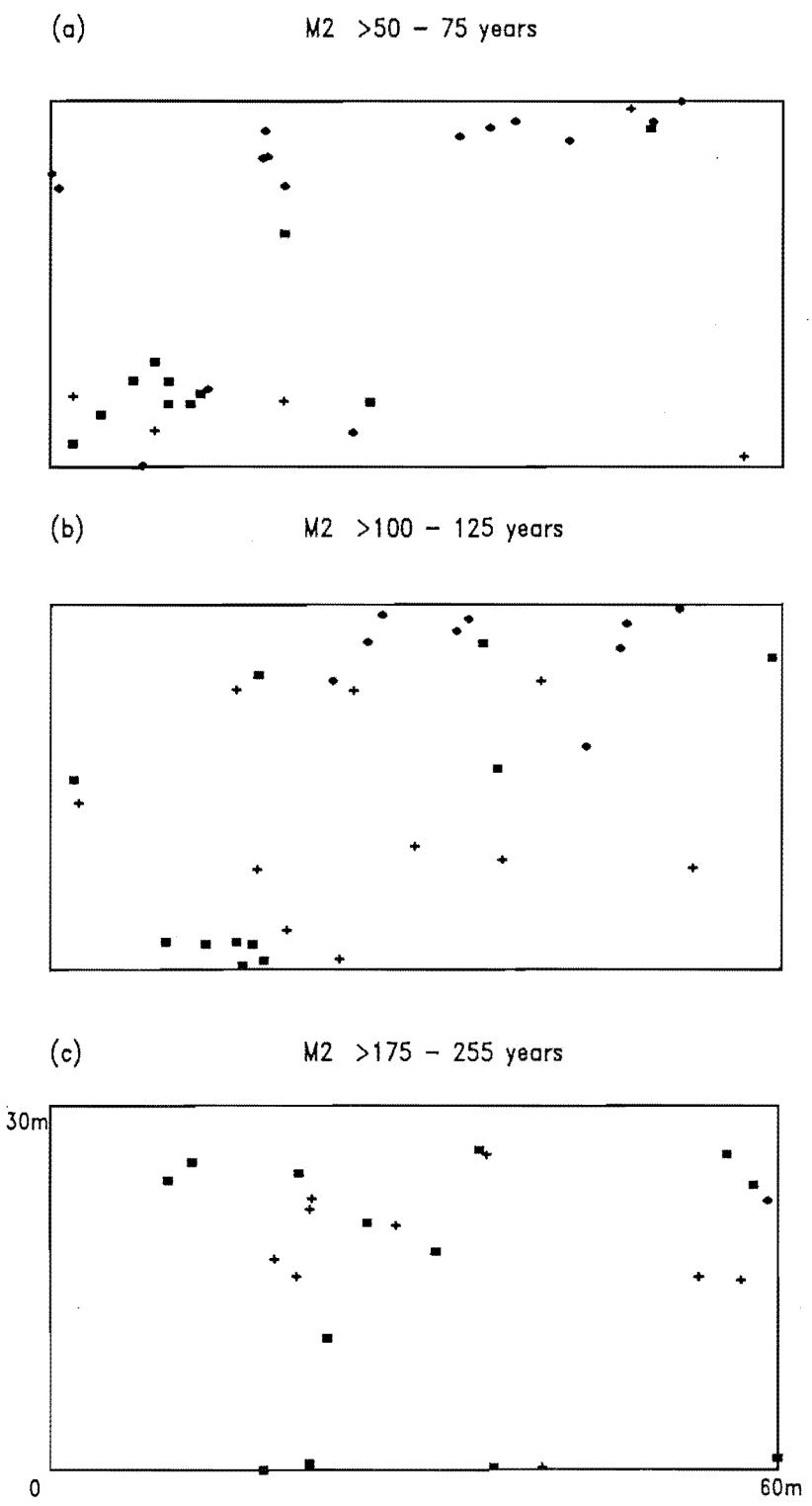
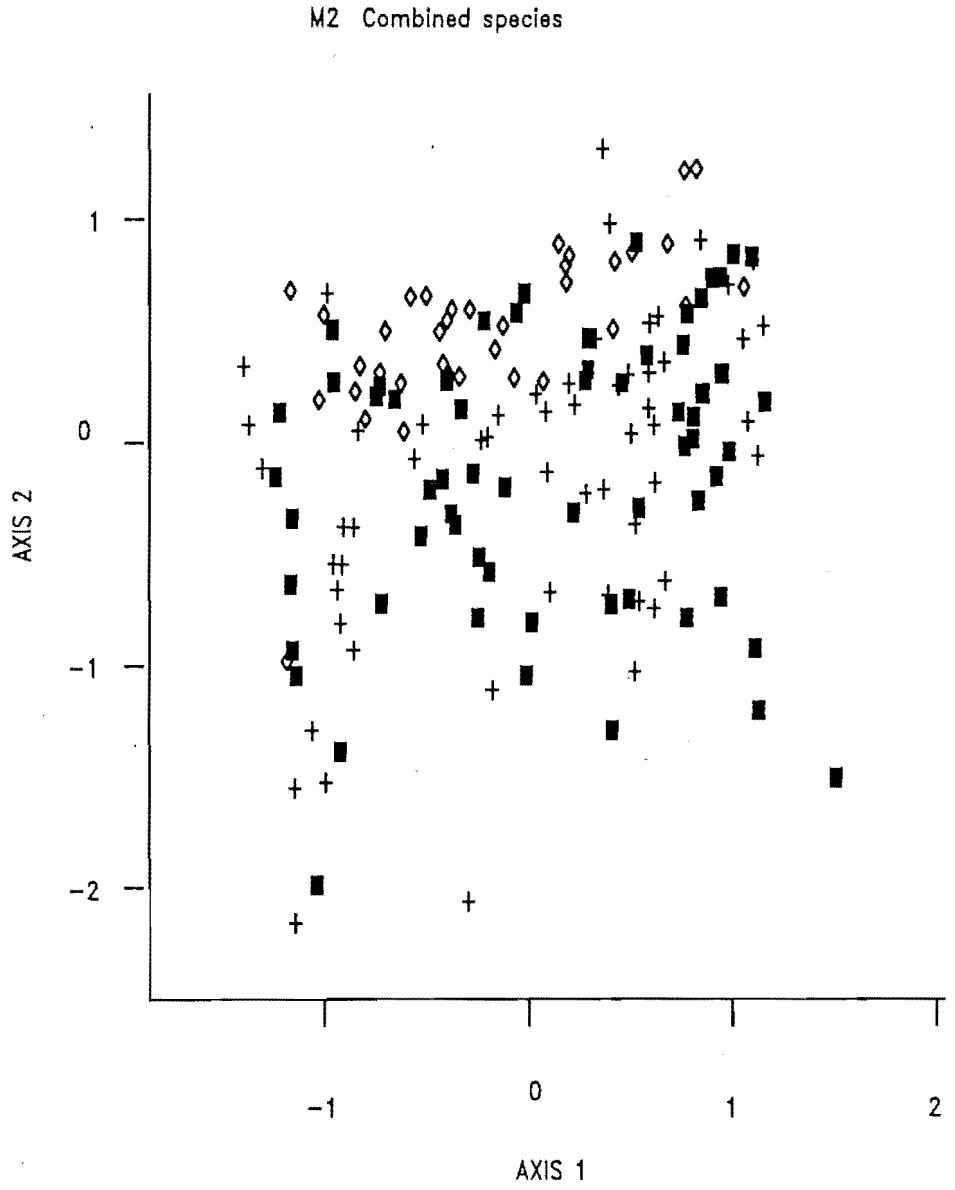


FIGURE 25: Scatter diagram obtained from an ordination of the association measure c_{ij}, reflecting tree age differences and spatial proximity, for all aged podocarp trees in stand M2. The symbols represent different species: ◊ = *Dacrycarpus dacrydioides*; ■ = *Dacrydium cupressinum*; + = *Prumnopitys ferruginea*.



patches. In the spatial correlogram, significant positive autocorrelation at distances up to 9 m (Fig 23a) reflected the establishment of trees in these localised patches. Patches of different size and age were scattered throughout the plot resulting in apparently random fluctuations in *z* values in distance classes 4 - 16 (>9 - 48 m). Significant negative autocorrelation in distance classes 17 - 20 (>48 - 60 m) was attributed to the patch of older trees at the eastern edge of the plot (Fig 24c) and younger trees along the western boundary.

When the three podocarp species were plotted separately on the ordination diagram (Fig 25) and in the age-class maps (Fig 24) further patterns were evident. *D. dacrydioides* and *P. ferruginea* tended to occur apart from each other in the ordination diagram, suggesting that these two species did not establish together in time or space. These patterns were evident in the age-class maps (Fig 24). *D. dacrydioides* and *P. ferruginea* tended to establish in different regions of the plot and *D. dacrydioides* dominated establishment in the younger age-classes. Single species clusters were also evident in the ordination diagram representing patches of trees of the same species.

Regeneration patterns

The majority of *Dacrycarpus dacrydioides* established in wet depressions in stand M2 (Table 15). Establishment patterns of *Dacrydium cupressinum*, *P. ferruginea*, and *W. racemosa* were significantly different (two-tailed Kolmogorov-Smirnov test; $P < 0.01$) with the majority of these species established on elevated or level sites. However, almost 30% of *D. cupressinum* ≥5 cm dbh established in wet depressions and trees ≥5 cm dbh tended to establish on level or elevated sites around the edges of depressions. Fewer *P. ferruginea* and *W. racemosa* ≥5 cm dbh established in wet depressions. Similarly fewer seedlings and saplings of all three podocarp species established in wet depressions and a greater percentage established on elevated sites.

TABLE 15: Percentage of trees (by species and size class) in establishment site and overhead cover classes in stand M2. D = depression, L = level, E1 = elevated >0.5 m, E2 = elevated 0.5 - 1 m, E3 = elevated >1 m; C = closed, I = intermediate, O = open. Sd+S = seedlings + saplings. n = number of trees measured. Only size-classes with >5 individuals are included.

	Establishment site					Overhead cover			
	D	L	E1	E2	E3	C	I	O	n
D.dacrydioides									
≥5cm dbh	78	17	5	0	0	30	14	56	36
Sd+S	62	24	8	6	0	84	14	2	50
D.cupressinum									
≥5cm dbh	29	37	17	14	3	25	20	55	65
Sd+S	6	30	24	26	14	88	8	4	257
P.ferruginea									
≥5cm dbh	12	49	14	21	4	44	9	47	57
Sd+S	1	31	20	38	10	87	7	6	81
W.racemosa									
≥5cm dbh	3	44	12	22	19	20	13	67	64

A large proportion of podocarp trees ≥5 cm dbh occurred in the closed or intermediate cover class in stand M2 (Table 15). This was attributed to the dominance of large-crowned *W. racemosa* in the canopy tiers (Table 1) which formed a more complete canopy cover than smaller crowned podocarp trees. *W. racemosa* had a greater proportion of trees occurring in the open cover class, reflecting its dominance in the canopy.

Disturbance history

Two large *D. cupressinum* > 95 cm dbh and two *P. ferruginea* > 325 years old appeared to be remnants of an older cohort of trees. In addition there were four snapped podocarp boles 69-160 cm dbh and associated log remnants in the plot. The size of these stumps suggested they were also members of a previously more extensive, older cohort.

There was no evidence of recent flood disturbance in the soil profiles of stand M2. On drier sites a dark brown Ah horizon overlaid a gleyed B horizon suggesting that soil development had proceeded unaffected by flood disturbance for at least 1000 years (Tonkin *et al.* 1985). In the absence of flooding the upsurge in podocarp regeneration commencing about 250 years ago probably occurred in response to openings formed by windthrow. Tree snaps and the presence of old mounds and log remnants supported this interpretation.

Establishment of the three podocarp species did not occur contemporaneously and podocarp regeneration in the last 250 years fluctuated with pulses of recruitment evident in the 175 - 200 year age-class in all three species, and in the 75 - 125 year age-classes in *P. ferruginea* and *D. dacrydioides*. Furthermore, tree recruitment was spatially patchy suggesting establishment in localised disturbance openings. Periods of establishment may have occurred in response to a series of disturbance openings formed by the windthrow of an older cohort of trees. Pulses in tree establishment evident over the past 250 years,

and recently windthrown and surviving emergent trees suggest that collapse of the original canopy occurred over an extended period.

The pulse of recruitment in the 175 - 200 year age class in stand M2 was synchronous with the pulse of *W. racemosa* and *D. cupressinum* recruitment in stand K2, suggesting that the disturbances were not just localised events.

Spatial patterns

Significant clumping of trees (Table 16) and significant spatial association among species (Table 17) can be attributed to the patchy distribution of establishment sites.

D. dacrydioides ≥ 5 cm dbh and *D. cupressinum* ≥ 5 cm dbh were positively associated. This reflects establishment of *D. dacrydioides* primarily in wet depressions, and *D. cupressinum* both in wet depressions and on level and elevated sites around depression edges. Positive association between *D. dacrydioides* ≥5 cm dbh and *D. dacrydioides* seedlings and saplings can be attributed to their similarity in microsite preferences (Table 15). In contrast, *D. cupressinum* seedlings and saplings established on level or elevated sites in drier areas of the plot and were negatively associated with *D. dacrydioides.*

Trees ≥5 cm dbh, and seedlings and saplings of *D. dacrydioides* and *D. cupressinum* were clumped at distances up to 20 m. At small scales clumping reflected the fine scale pattern of microrelief and patchiness in the distribution of disturbance openings. At larger scales clumping was attributed to broad scale drainage patterns; wet depressions were distributed patchily throughout the plot.

P. ferruginea established primarily on level and elevated sites in drier parts of the plot. *P. ferruginea* ≥5 cm dbh were negatively associated with both *D. dacrydioides* and

D. cupressinum ≥5 cm dbh that established in and around wet depressions. *P. ferruginea* seedlings and saplings had similar establishment site preferences to *D. cupressinum* seedlings and saplings (Table 15) and this was reflected in their significant positive association.

Large *W. racemosa* (≥ 20 cm dbh) also established on drier, level or elevated sites and were positively associated with *P. ferruginea* and negatively associated with *D. dacrydioides*. However, *W. racemosa* ≥ 20 cm dbh were also positively associated with *D. cupressinum* ≥ 5 cm dbh, which tended to occur around wetter sites. This positive association was attributed to clumping of *D. cupressinum* around large, senescent *W. racemosa*, and the establishment of *W. racemosa* beneath the two large *D. cupressinum* trees. Small *W. racemosa* (< 20 cm dbh) established on similar sites to *D. cupressinum* seedlings and saplings and the two were positively associated.

Clumping of *P. ferruginea* seedlings and saplings, and trees ≥5 cm dbh was attributed to the patchy distribution of suitable establishment sites and, at larger scales, to *P. ferruginea's* preference for drier areas of the plot. Clumping of *W. racemosa* <20 cm dbh at small distances was attributed to the patchy distribution of suitable establishment sites and establishment in canopy gaps.

W. racemosa ≥20 cm dbh were randomly distributed throughout the plot. This may reflect thinning of tree clumps in canopy gaps and a scattered distribution of canopy openings throughout the stand.

TABLE 16: Patterns of spatial dispersion for trees (by species and size-class) in stand M2. Letters indicate significant ($P < 0.05$) deviation from a random distribution at distance t based on values of the function *L(t)*; U = uniform distribution, C = clumped distribution, . = random. Sd+S = seedlings + saplings, n = number of individuals in each size-class.

	t (metres)																				n
	1			5					10								15				
D.dacrydioides																					
≥5cm dbh	C	C		C	C	C	C	C	C	C	C	C	C	C	C	C	C				36
Sd + S	C	C		C	C	C	C	C	C	C	C	C	C	C	C	C	.				50
D.cupressinum																					
≥5cm dbh	C	C		C	C	C	C	C	C	C	C	C	C	C	C	C	C				64
Sd + S	C	C		C	C	C	C	C	C	C	C	C	C	C	C	C	C				257
P.ferruginea																					
≥5cm dbh	.	.		.	C	C	C	C	C	C	C	C	C	C	C	C	.				57
Sd + S	C	C		C	C	C	C	C	C	C	C	C	C	C	C	C	C				81
W.racemosa																					
<20cm dbh	.	C		C	C	C	C	.	C	C	.	.	.	.	.	.	.				36
≥20cm dbh	.	.		.	.	.	.	.	.	.	.	.	.	.	.	.	.				28

TABLE 17: Patterns of association for trees (by species and size-class) in stand M2 derived from the function $L_{12}(t)$. + and - denote significant ($P < 0.05$) positive and negative association for distances of t up to 5 m, . = no significant association. Sd+S = seedlings + saplings. Only size-classes with >10 individuals were analysed.

	D.dac Sd+S	*D.cup* ≥5cm	*D.cup* Sd+S	*P.fer* ≥5cm	*P.fer* Sd+S	*W.rac* <20cm	*W.rac* ≥20cm
D.dacrydioides, ≥5cm dbh	+	+	–	–	.	.	–
D.dacrydioides, Sd+S		.	–	–	.	.	–
D.cupressinum, ≥5cm dbh			.	–	.	–	+
D.cupressinum, Sd+S				.	+	+	.
P.ferruginea, ≥5cm dbh					.	.	+
P.ferruginea, Sd+S						.	+
W.racemosa, <20cm dbh							.

STAND M1

Stand structure

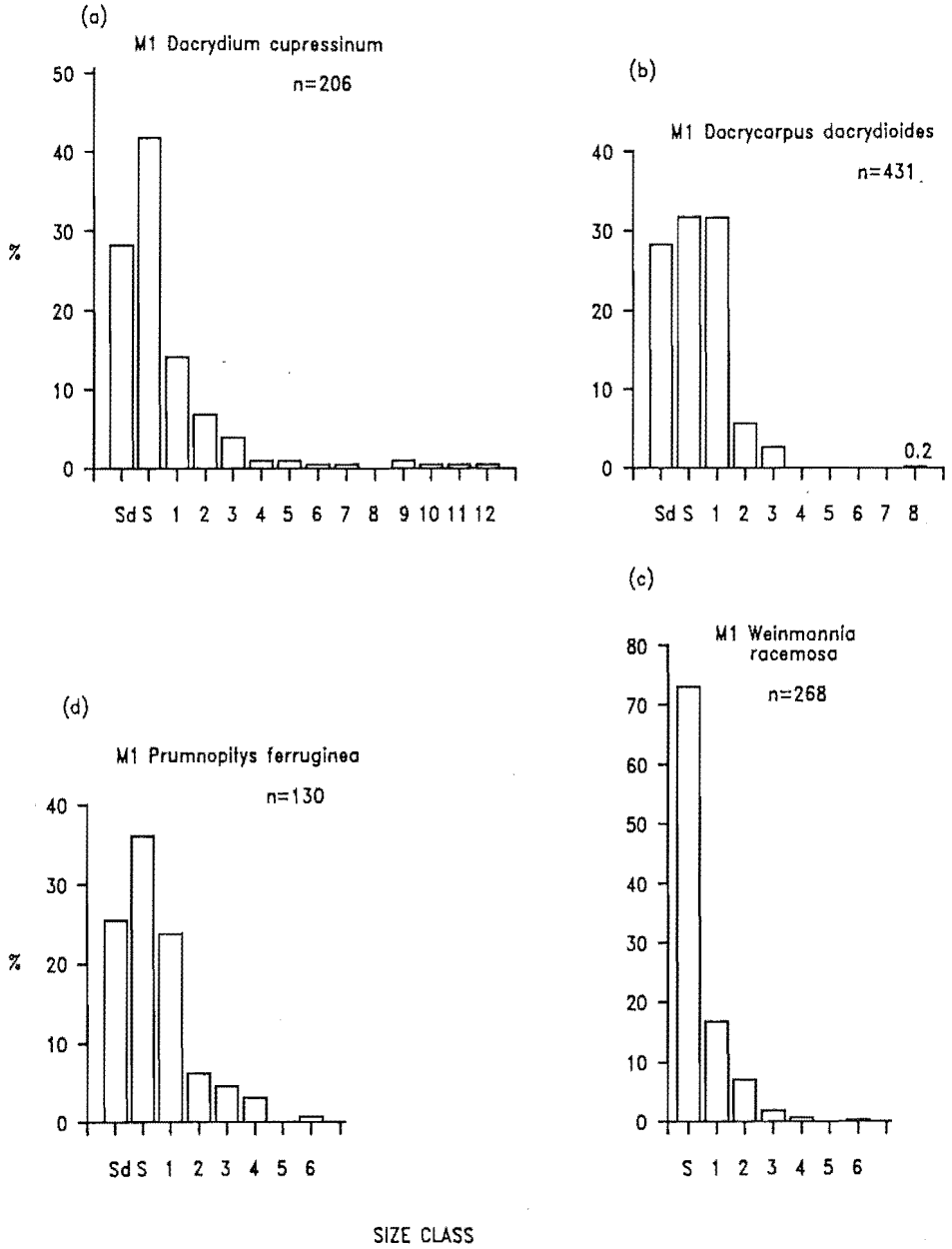
I did not core trees in stand M1 for construction of age distributions because of the large number of stems in the plot (Table 1) and because >80% of trees were <15 cm dbh and so were likely to be of a similar, young age. Estimates of tree ages were obtained from best fit regressions of age against diameter (Table 2). These were derived from random samples of trees cored in stand M1, for *D. dacrydioides* and *D. cupressinum*, and from trees cored in nearby stand M2, for *P. ferruginea* and *W. racemosa*. Interpretation of population dynamics and disturbance history are based primarily on size structures and comparisons with nearby stand M2.

Species size-class distributions resembled reverse J-shaped curves (Fig 26). However, discontinuities were evident in the size structures of all four species. Increased recruitment in the smaller size-classes probably occurred in response to disturbance (cf., stand M2).

There was a single large *Dacrycarpus dacrydioides* tree 78 cm dbh in stand M1. The remaining *D. dacrydioides* trees were all <35 cm dbh. The age-diameter regression for *D. dacrydioides* in stand M1 (Table 2) gave an age of 138 years for a 35 cm tree suggesting that the majority of *D. dacrydioides* in the plot were <140 years old. *D. dacrydioides* <35 cm dbh were abundant in stand M1.

The size class distribution of *Dacrydium cupressinum* showed a discontinuous pattern of recruitment with five trees >85 cm dbh comprising an older cohort. Two of these trees, measuring 90.5 and 91 cm dbh, were cored and their ages estimated as 444 and 513 years respectively. Over 90% of *D. cupressinum* were <35 cm dbh. The age-diameter regression for *D. cupressinum* in stand M1 (Table 2) gave an estimated age of

FIGURE 26: Size- and age-class frequency distributions for the main species in stand M2. n = number of trees. Size classes are: Sd = seedlings (≥0.5 m but <1.3 m tall); S = saplings (≥1.3 m tall but <5 cm dbh); 1 = 5 - 14.5 cm dbh; 2 = 15 - 24.5 cm dbh; 3 = 25 - 34.5 cm dbh etc.



223 years for a 35 cm dbh tree which suggested that the majority of *D. cupressinum* were less than 225 years old.

One *Prumnopitys ferruginea* was >45 cm dbh. The relationship between age and diameter for *P. ferruginea* in nearby stand M2 indicated that the trees <45 cm dbh were likely to be <270 years old.

The size-class distribution of *W. racemosa* also indicated a discontinuous pattern of recruitment. There was a single tree 62 cm dbh while the remainder were <45 cm dbh. The relationship between age and diameter for *W. racemosa* in stand M2 gave an estimated age of 212 years for a 45 cm dbh tree.

Regeneration Patterns

The four species differed in their patterns of establishment on different sites (Table 18). *Dacrycarpus dacrydioides* established primarily in wet depressions with very few individuals establishing on elevated sites. Both *D. cupressinum* and *P. ferruginea* established predominantly on level or low elevated sites (<0.5 m above the ground). *D. cupressinum* showed a greater tendency to establish in wet depressions while more *P. ferruginea* established on elevated sites. No *Weinmannia racemosa* established in wet depressions and 61% established on elevated sites ≥0.5 m above the ground.

In all species size-class groups, except *P. ferruginea* seedlings and saplings, the majority of trees occurred in the open or intermediate overhead cover class (Table 18). This was attributed to the lack of an intact canopy and the reduced abundance of *W. racemosa* in the upper canopy tier (Table 1; cf., stand M2). The large, emergent podocarp trees were scattered throughout the plot and podocarps in the denser lower tiers had small crowns, characteristic of young rapidly growing trees, that formed a relatively open cover.

TABLE 18: Percentage of trees (by species and size-class) in establishment site and overhead cover classes in stand M1. D = depression, L = level, E1 = elevated >0.5 m, E2 = elevated 0.5 - 1 m, E3 = elevated >1 m; C = closed, I = intermediate, O = open. Sd+S = seedlings + saplings. n = number of trees measured. Only size-classes with >5 individuals are included.

	Establishment site					Overhead cover			
	D	L	E1	E2	E3	C	I	O	n
D.dacrydioides									
≥5cm dbh	76	20	3	1	0	7	33	60	172
Sd+S	86	13	1	0	0	38	40	22	259
D.cupressinum									
≥5cm dbh	13	54	22	7	4	5	10	85	62
Sd+S	18	35	33	14	0	27	48	25	144
P.ferruginea									
≥5cm dbh	3	45	21	10	21	4	48	48	50
Sd+S	0	54	21	21	4	60	26	14	80
W.racemosa									
≥5cm dbh	0	13	26	17	44	7	39	54	72

Disturbance history

The five large *D. cupressinum* trees, and the single large *D. dacrydioides* and *P. ferruginea* appeared to be remnants of an older cohort of trees (cf., stand M2). Soil profiles on drier sites in stand M1 were similar to those in adjacent stand M2, with no evidence of recent flood disturbance. Furthermore, there was evidence of past windthrow in the presence of old mounds and a large stump >80 cm dbh.

Age estimates obtained from age-diameter regressions indicated that the upsurge in recruitment evident in the size-class distributions in stand M1 was approximately synchronous with that occurring in stand M2. Similarities between stands M1 and M2 in species size distributions suggest that patterns of recruitment in the two stands were similar and may have occurred in response to a similar pattern of disturbance. The large trees in stand M1 may be the survivors of a previously more extensive canopy that has been affected by wind disturbance, with canopy collapse occurring over an extended period.

Spatial patterns

The spatial dispersion of trees (Table 19) and spatial association among species (Table 20) reflected species establishment site preferences.

Dacrycarpus dacrydioides ≥ 5 cm dbh and *D. dacrydioides* seedlings and saplings both established predominantly in wet depressions and were positively associated. The two *D. dacrydioides* size-classes were clumped at distances up to 15 m reflecting the patchy distribution of wet depressions and possibly establishment in localised disturbance openings. In stand M1 wet depressions were larger than in stand M2 which resulted in large clumps of *D. dacrydioides* stems.

Dacrydium cupressinum ≥ 5 cm dbh and *D. dacrydioides* seedlings and saplings

were negatively associated. This was attributed to establishment of *D. dacrydioides* in extensive areas of wet depressions and *D. cupressinum* predominantly on level or elevated sites around the edges of depressions or in drier parts of the plot. In contrast *D. cupressinum* seedlings and saplings were positively associated with *D. dacrydioides* ≥ 5 cm dbh. Small clumps of *D. cupressinum* often established on elevated sites in the extensive wet depressions, in addition to establishing throughout the stand on drier level and elevated sites.

Both *Prumnopitys ferruginea* and *Weinmannia racemosa* were negatively associated with *D. dacrydioides* and *D. cupressinum*. *P. ferruginea* and *W. racemosa* established on level and elevated sites in drier parts of the plot and avoided wet depressions.

Clumping of *D. cupressinum*, *P. ferruginea*, and *W. racemosa* reflected the patchy distribution of suitable establishment sites as a consequence of both small-scale topographic variation and the patchy distribution of localised disturbance openings (cf., stand M2).

TABLE 19: Patterns of spatial dispersion for trees (by species and size-class) in stand M1. Letters indicate significant ($P < 0.05$) deviation from a random distribution at distance t based on values of the function *L(t)*; U = uniform distribution, C = clumped distribution, . = random. Sd+S = seedlings + saplings, n = number of individuals in each size-class.

	t (metres)																				n
	1			5					10							15					
D.dacrydioides																					
≥5cm dbh	C	C		C	C	C	C	C	C	C	C	C	C	C	C	C					172
Sd + S	C	C		C	C	C	C	C	C	C	C	C	C	C	C	C					259
D.cupressinum																					
≥5cm dbh	C	C		C	C	C	C	C	C	C	C	C	C	C	C	C					62
Sd + S	C	C		C	C	C	C	C	C	C	C	C	C	C	C	.					144
P.ferruginea																					
≥5cm dbh	C	.	.	C	C	C	C	C	C	.	.	.	.	.	.	.					50
Sd + S	C	C		C	C	C	C	C	C	C	C	C	C	.	.	.					80
W.racemosa																					
≥5cm dbh	C	.	.	C	C	C	C	C	C	C	.	C	.	.	.						72

TABLE 20: Patterns of association for trees (by species and size-class) in stand M1 derived from the function $L_{12}(t)$. + and - denote significant ($P < 0.05$) positive and negative association for distances of t up to 5 m, . = no significant association. Sd+S = seedlings + saplings. Only size-classes with >10 individuals were analysed.

	D.dac Sd+S	*D.cup* ≥5cm	*D.cup* Sd+S	*P.fer* ≥5cm	*P.fer* Sd+S	*W.rac* ≥5cm
D.dacrydioides, ≥5cm dbh	+	.	+	–	.	–
D.dacrydioides, Sd+S		–	.	–	.	–
D.cupressinum, ≥5cm dbh			.	.	+	–
D.cupressinum, Sd+S				–	.	.
P.ferruginea, ≥5cm dbh					.	.
P.ferruginea, Sd+S						.

CHAPTER VI

DISCUSSION

DIFFERENCES IN SPECIES REGENERATION PATTERNS

There have been few autecological studies of the New Zealand Podocarpaceae, especially comparative studies. Ecological characteristics of the species have largely been inferred from synecological studies (eg., Cockayne 1928; June 1982; McDonald 1989).

In the present study, differences among species in their occurrence in overhead cover classes, relative abundance in different height tiers, and numbers of dead standing trees suggested differences in species relative shade tolerance (see page 54). Furthermore, species establishment site preferences and stem spatial distributions showed that species differed in their patterns of establishment on different forest floor microsites. In this section I discuss these differences in species regeneration patterns and consider their implications for the maintenance of species diversity in lowland podocarp forests.

Relative shade tolerance

The order of relative shade tolerance inferred from this study (*P. ferruginea* > *D. cupressinum* > *D. dacrydioides*) concurs with the observations of previous authors (June 1982; Beveridge 1983; Smale & Kimberley 1986). Furthermore, patterns of regeneration in patches of different size suggest that the three podocarp species differ in their ability to exploit canopy openings of different size, in relation to their relative shade tolerance.

Light demanding *D. dacrydioides* required large openings in the podocarp canopy, formed by floods or extensive overstorey collapse, for successful regeneration. While *D. dacrydioides* could establish beneath an intact podocarp canopy (seedlings and saplings

were common in stands K2 and F2), no trees grew beyond the sapling stage in the absence of major disturbance (see also Wardle 1974; Smale 1984). Furthermore, within large canopy openings *D. dacrydioides* established away from existing canopy cover. In stand F2 *D. dacrydioides* 150 - 242 years old established as a distinct patch in the centre of the large disturbance opening (Fig 17b). This pattern of establishment may reflect variation in the light environment within the canopy gap. Total incident radiation is higher in gap centres than in gap-forest edges (eg., Denslow *et al.* 1990).

In contrast, shade tolerant *P. ferruginea* can grow in small canopy gaps (Beveridge 1983; Smale & Kimberley 1986). In the present study it regenerated beneath an existing podocarp canopy, and around the edges of large disturbance openings (eg., stands K2 and F2). In lowland podocarp forest in south Westland *P. ferruginea* is characteristically a subcanopy tree (Wardle 1977; Duncan *et al.* 1990; Norton & Leathwick 1990) and the majority of *P. ferruginea* in the present study were in the closed overhead cover class. Gaps are important for growth to maturity in podocarp-broadleaved forest in the central North Island (Smale & Kimberley 1986) and *P. ferruginea* established in response to disturbance in the present study. Small ephemeral openings or side lighting from adjacent gaps may be important for successful growth to maturity of trees established beneath an existing podocarp canopy (R. Duncan *personal observation*).

D. cupressinum occasionally recruited into small openings beneath a relatively intact podocarp canopy (eg., stands K2 and F2). The majority of trees, however, established after more extensive removal of the podocarp overstorey (see also Hutchinson 1928, 1932; Poole 1937; Six Dijkstra *et al.* 1985). Occasional recruitment of *Dacrydium cupressinum* in small canopy openings concurs with its status as intermediate in shade tolerance between *P. ferruginea* and *D. dacrydioides.*

Growth rates of the three podocarp species are consistent with the general

strategies associated with small versus large gap specialists (Bazzaz & Pickett 1980). The slow radial growth rate of *P. ferruginea* (Table 1) and its ability to grow at low light levels (Beveridge 1983) are characteristics of species specializing in small gaps (Bazzaz & Pickett 1980; Swaine & Whitmore 1988; Canham 1989). In contrast, large gap specialists such as *D. dacrydioides* require high resource levels and have faster growth rates (Table 1; Bazzaz & Pickett 1980). The intermediate status of *D. cupressinum* was reflected in its intermediate rate of growth (Table 1).

W. racemosa is considered relatively light demanding (Cockayne 1928) and less shade tolerant than *D. cupressinum* (June 1982). Despite this it regenerated abundantly in small canopy gaps (eg., stands K2, F1 and F2; see also Stewart & Veblen 1982; June 1982; Stewart 1986b). The ability of *W. racemosa* to sprout vegetatively from both live and damaged individuals (Wardle 1966) may contribute to its successful colonisation of small canopy openings (June 1982; Stewart 1986b).

Microsite preferences

Variation in forest floor microrelief occurred for a number of reasons. Topography influenced the patterns of drainage and the distribution and abundance of wet depressions within stands. Plots located in low-lying hollows were poorly drained and had abundant wet depressions (eg., stand M1; Table 3). Flooding (in stands F1 and F2) and treefalls left logs and stumps on the forest floor that formed elevated sites. Accumulated woody debris and organic material around the bases of large podocarp trees also formed elevated mounds. Uprooting of trees characteristically forms a pit and mound microtopography with upturned root plates forming elevated sites adjacent to pits (Stephens 1956; Schaetzl *et al.* 1989).

Microrelief can influence plant distributions (Hutnik 1952; Henry & Swan 1974; Bratton 1976; Hicks 1980; Thompson 1980; Lawton & Putz 1988; Peterson *et al.* 1990).

Species preferences for particular microsites may reflect the environmental variation associated with microrelief (Snaydon 1962; Mott & McComb 1974; Beatty 1984). Experimental studies have shown fine-scale differences among species in their ability to establish in contrasting microhabitats (Gross & Werner 1982; Fowler 1982).

The four species in the present study responded strongly to differences in forest floor microrelief. Differences among species in their patterns of establishment may reflect the response of species to different environmental conditions associated with different microsites.

Level sites in recently flooded stands (stands K1, K2, F1 and F2) were predominantly exposed mineral soil. These young surfaces are relatively fertile (Sowden 1986) and in stands K2, F1, and F2 were often inundated with water for periods of days following heavy rainfall (R. Duncan *personal observation*). In contrast, elevated sites are likely to be drier (Adams & Norton 1991; see also Beatty 1984) and compared with recent mineral soils, are probably poorer in nutrients.

D. dacrydioides may have a competitive advantage on level, mineral soil sites as a consequence of its relatively high nutrient uptake ability (Hawkins & Sweet 1989) and faster growth rate (Table 1). Moreover, *D. dacrydioides* is tolerant of saturated soil conditions but may be unable to establish on drier elevated sites as seedling mortality is high or complete if sites are not permanently moist (Hinds & Reid 1957). In contrast *D. cupressinum*, *W. racemosa*, and *P. ferruginea* commonly establish on elevated sites (Wardle 1966; Franklin 1968; June 1982; Stewart 1986b).

Species microsite preferences were different in stands on older surfaces (stands M1 and M2) compared with the stands on younger flood deposits. On older surfaces *D. dacrydioides* was confined to wet depressions while the other three species established

mainly on level or elevated sites. *D. cupressinum* was the only other species that tended to establish in and around wet depressions (see also June 1982).

Moisture may be a factor limiting *D. dacrydioides* establishment to wet depressions. On older surfaces, level sites were covered with bryophytes and litter (R. Duncan *personal observation*) in which established seedlings may be susceptible to desiccation during dry periods (eg., Cameron 1963). Moreover, wet depressions often had areas of exposed mineral soil that may favour *D. dacrydioides* establishment.

While *D. cupressinum* is capable of growing in very wet soils it is unable to tolerate permanent waterlogging until a surface layer of humus has accumulated (Hinds & Reid 1957). *P. ferruginea* and especially *W. racemosa* established almost exclusively on level or elevated sites and avoided poorly drained areas.

Because of variation in vegetative cover, contrasting microsites may have different light environments (Lawton & Putz 1988; Uhl *et al.* 1988). In poorly drained sites the abundance and vigour of tree ferns and broadleaf species are reduced (Veblen & Stewart 1982) which may result in locally elevated light levels. Establishment of *Dacrycarpus dacrydioides* in wet depressions, and *Dacrydium cupressinum* around the edges of wet depressions may reflect the lack of competition at these sites. The dominance of podocarp species on suboptimal sites has commonly been attributed to their inability to compete with broadleaved species on better sites (Hinds & Reid 1957; Wardle 1974).

Establishment on elevated sites may also be a means of avoiding competition with understorey plants by establishing above competing vegetation (Ogden 1985a). There was a marked tendency for *D. cupressinum* seedlings and saplings to establish on higher microsites than trees ≥5 cm dbh in stand F2 (Table 12). This change in establishment height may reflect changes in understorey conditions. The majority of trees ≥5 cm dbh

established in canopy openings formed by flood disturbance, probably in relatively open sites. In contrast, the present population of seedlings and saplings established beneath a podocarp canopy and in competition with a well developed understorey.

Apart from a differential response to environmental variation associated with forest floor microrelief, two other mechanisms could account for species observed microsite preferences (Beatty 1984). These mechanisms are: (1) differential patterns of seed dispersal, and (2) selective mortality in different microsites due to herbivory or pathogens.

The distribution of species in contrasting microsites could reflect the patterns of seed dispersal as well as the suitability of sites for establishment and growth (eg., Thompson 1980; Peterson *et al.* 1990). Podocarp seedlings, notably *D. cupressinum*, often establish beneath large, senescent *W. racemosa* (Cameron 1954; Beveridge 1973). This pattern of establishment has been attributed to two causes. First, a gradually opening broadleaf overstorey may provide favourable light conditions for podocarp regeneration (Beveridge 1983). Second, large *W. racemosa* are used as perch trees by kereru (New Zealand wood pigeon; *Hemiphaga novaeseelandiae*) which disperse podocarp seed. Clumping of seedlings beneath *W. racemosa* may reflect the patterns of seed dispersal by birds (Beveridge 1964, 1973; McEwen 1978).

Establishment of *D. cupressinum* beneath large *W. racemosa* in the present study (eg., stand M2) could in part be due to the patterns of seed dispersal by birds. However, the distribution of podocarp species in contrasting microsites could not be attributed to differential patterns of dispersal. All three podocarp species are dispersed by kereru (McEwen 1978). Nevertheless, birds are critical for the effective spread of podocarp propagules as seed can be blown a maximum distance of about 40 m from parent trees (Beveridge 1964). Colonisation of large or isolated disturbance patches must be primarily by bird dispersal. The establishment of a suitable vegetative cover on open sites may be

a prerequisite to attracting birds with podocarp seed (Wardle 1974).

There is little information on the causes of tree mortality to assess the hypothesis that selective herbivory or pathogen attack in particular microsites influences tree distributions. Fungal pathogens kill *D. cupressinum* seedlings (June 1982) and *D. dacrydioides* seedlings are defoliated by insects on some sites (Beveridge 1983). However, insect or fungal attacks are not considered a major cause of podocarp seedling mortality (Beveridge 1983). Insects, birds, and introduced rodents destroy podocarp seed (Beveridge 1964). There is, however, no evidence to suggest selective predation of different species in contrasting microsites.

Maintenance of species diversity

The four species in the present study partition establishment sites along gradients related to surface microrelief and canopy cover. Each species appears to have a competitive advantage in at least one type of establishment site. In a heterogeneous environment partitioning of establishment sites may contribute to the coexistence of the four species (Denslow 1985).

Disturbance appears critical to the maintenance of species diversity as it is the source of much of the environmental variation to which species differentially respond (see Discussion below). While gap size has been viewed as a principle axis of differentiation among species (Denslow 1980) other characteristics of disturbance openings are a further source of heterogeneity to which species differentially respond (Orians 1982; Schaetzl *et al.* 1989). In lowland podocarp forests partitioning of forest floor microsites may contribute to the maintenance of species diversity (see also Núñez-Farfán & Dirzo 1988; Peterson *et al.* 1990).

DETERMINANTS OF PATCH COMPOSITION AND STRUCTURE

Intermittent past disturbances affected all six of the stands studied. Disturbances of different type and intensity formed canopy openings that differed in a number of characteristics that influenced the composition and structure of regenerating patches. In particular, the size of canopy openings and surface microrelief were important determinants of subsequent forest establishment. In this section I discuss how characteristics of disturbance openings interact with species regeneration requirements to determine resulting patch composition.

Flood disturbance

Relatively even-aged recruitment of canopy trees into openings formed by flood disturbance indicated that much of the composition and structure of regenerating patches was determined at patch initiation (cf., 'initial floristic composition', Egler 1954). Floods formed extensive, continuous canopy openings that favoured regeneration of the more light demanding podocarps, *D. dacrydioides* and *D. cupressinum*. Following flooding, *P. ferruginea* and *W. racemosa* established primarily around gap edges, or beneath the surviving or regenerating canopy.

The intensity of flood disturbance influenced surface microrelief and hence subsequent forest establishment. Severe flooding removed all vegetation and left relatively homogeneous deposits of silt. Establishment on these surfaces was dominated by *D. dacrydioides* (eg., stands K1 and K2). Mixed canopy stands established after less intense flood disturbance which left exposed logs and stumps, providing sites for establishment of *D. cupressinum*, *P. ferruginea*, and *W. racemosa* (eg., stands F1 and F2).

A number of studies have shown that floristic composition varies among canopy openings of different size (eg., Hibbs 1982; Brokaw 1985; Phillips & Shure 1990). The

distribution and frequency of creation of different sized openings therefore has important consequences for overall forest composition and vegetation patterns. However, fewer studies have examined the distribution of species within a given canopy gap.

Variation in the patterns of regeneration in different regions of canopy openings was evident in the present study (eg., stand F2). This variation was related to patterns in surface microrelief and surviving canopy cover. Because flooding can form extensive canopy openings, within-gap environmental heterogeneity is an important determinant of forest composition and structure in lowland podocarp forests.

Recruitment into openings formed by flooding occurred over long time intervals (c. 100 - 300 years). Slow colonization of disturbance openings is a possible explanation (cf., Franklin & Hemstrom 1981). Destruction of vegetation by floods could remove seed sources over large areas and podocarps are reliant on birds for dispersal of seeds over distances of greater than 40 m (Beveridge 1964). Successful dispersal onto recently flooded sites may be dependent on the development of a shrub cover to attract seed dispersing birds (Wardle 1974), which is likely to delay podocarp establishment.

Wind disturbance

Openings formed by treefall differ from those formed by flood disturbance (Salo *et al.* 1986) and favour regeneration of different species. Contemporaneous establishment of species in stands affected by flooding suggested that the floods were discrete, punctuated events that formed extensive, continuous openings. In contrast treefall openings were smaller and more scattered. Even in stands M1 and M2, where regeneration occurred in response to extensive overstorey collapse, asynchronous establishment of species and the patchy distribution of tree ages suggested establishment occurred in scattered treefall openings.

The intensity of windstorm events is likely to influence the degree of canopy opening (Canham & Loucks 1984) and hence subsequent forest establishment. *Weinmannia racemosa* dominated regeneration in scattered, small openings formed in a relatively intact podocarp canopy in stand K2 (c. 175 - 200 years ago). In contrast, all four species established after collapse of the podocarp canopy in stands M1 and M2.

In stand M2 the three podocarp species established at different times and in different areas of plot. This may in part reflect the spatial and temporal patterns of treefall. Recruitment of shade intolerant *D. dacrydioides*, commencing about 125 years ago in stands M1 and M2, may have been initiated by a period of more extensive overstorey collapse, forming larger openings.

Understorey plants can survive in openings formed by treefall but are less likely to survive in openings formed by floods, where understorey vegetation is removed. Suppressed seedlings and saplings of canopy species that survive disturbance may have an advantage in colonising treefall openings (Oliver & Larson 1990). The ability of *P. ferruginea* to establish and grow beneath an intact podocarp canopy (June 1982; Beveridge 1983) may give it an advantage in colonising treefall gaps. Similarly, the dominance of *W. racemosa* in treefall openings on drier sites may in part be due its ability to vegetatively resprout. This would favour its persistence in treefall gaps as opposed to openings formed by flood disturbance, where physical damage to trees may be more severe.

Understorey plants that survive in treefall gaps, and fast growing species that rapidly colonise openings compete with seedlings of canopy species for resources, or can alter gap microenvironments and so prevent subsequent establishment of canopy trees (Veblen 1982; Huenneke 1983). Broadleaved species, particularly *W. racemosa*, and tree ferns grow rapidly in openings formed by wind disturbance in *D. cupressinum* dominated

forest in south Westland (Poole 1937). Seedlings of *D. cupressinum* and *P. ferruginea* present as suppressed individuals, or that establish after disturbance, are able to grow beneath the faster growing broadleaf overstorey (eg., stand M2) eventually overtopping and suppressing the broadleaf trees (Poole 1937; Six Dijkstra *et al.* 1985).

Dacrycarpus dacrydioides can grow beneath a shrub canopy on recent flood deposits (Wardle 1974). However, it appears unable to establish beneath a more vigourous tree fern and *W. racemosa* overstorey in smaller treefall gaps. The restriction of *D. dacrydioides* to wet depressions on older surfaces may reflect sites where competition from broadleaf species, particularly *W. racemosa*, is reduced.

Gaps formed by treefalls further favour regeneration of *D. cupressinum*, *P. ferruginea*, and *W. racemosa* because fallen logs, stumps, and uproot mounds provide preferred establishment sites for these species. Putz (1983) suggested that mounds formed by tree uprooting may similarly favour regeneration of pioneer species in tropical treefall gaps because uproot mounds are preferred establishment sites for some pioneer species.

Environmental gradients

The type and intensity of disturbance influenced gap characteristics such as gap size, the amount of surviving vegetation, and the nature of the surface microrelief. Broad-scale environmental gradients also influenced gap environments and were important determinants of patch composition.

Regeneration of *D. dacrydioides* on older surfaces required openings to coincide with wet depressions. Underlying drainage gradients therefore affected the composition of openings in stands M1 and M2. Regeneration on the drier site (stand M2) was dominated by *D. cupressinum*, *P. ferruginea*, and *W. racemosa*, reflecting the

predominance of better drained level and elevated microsites. In contrast *D. dacrydioides* dominated regeneration in poorer drained stand M1 that had abundant wet depressions.

Soil drainage gradients may influence the long term patterns of forest succession (Wardle 1980a). Swamp forest dominated by *D. dacrydioides* (open kahikatea forest transitional to swamps [Wardle 1977]; [kahikatea]/(*Myrsine*) forest [Duncan *et al.* 1990]) may develop in poorly drained hollows where fertility is maintained through periodic siltation (Wardle 1974, 1980a; Duncan *et al.* 1990).

Changes in soil properties with time (see Tonkin *et al.* 1985) are likely to affect the composition of regenerating patches on old surfaces. Soil drainage deteriorates with time (Tonkin *et al.* 1985; Sowden 1986) which should favour recruitment of *D. dacrydioides.* However, this is offset by accumulations of organic matter, reductions in the area of exposed mineral soil, and an increase in the cover of elevated sites, all of which favour establishment of *D. cupressinum*, *P. ferruginea*, and *W. racemosa.* In the absence of periodic siltation declining nutrient levels (Sowden 1986) may also give *D. cupressinum* a competitive advantage in nutrient uptake over *D. dacrydioides* (Hawkins & Sweet 1989).

The impact of a disturbance may vary from place to place on the landscape as a consequence of variation in landform and broad-scale vegetation patterns (eg., Foster 1988). The size of windthrow openings in *D. cupressinum* dominated forest has been related to variation in topography and soils (James 1987). More extensive blowdowns occur on flat, poorly drained sites. *W. racemosa* regenerates vigorously in small treefall gaps on drier sites (eg., stand M2) and this may account for its dominance on better drained hill slopes (see for example Norton & Leathwick 1990). In contrast, the vigour of *W. racemosa* is reduced on poorer drained, older terraces (eg., stand M1) where large windfall openings, and poor drainage would favour regeneration of podocarps.

FOREST SUCCESSION

Vegetation change following flood disturbance in the present study followed the generalized successional sequence described for even-aged patches of trees established after disturbance in northern temperate forests (Oliver 1981; Peet & Christensen 1987; Oliver & Larson 1990). Establishment of podocarps commenced after flood disturbance, reached a peak and then declined as regeneration was inhibited by canopy closure. In dense stands of *Dacrycarpus dacrydioides* continued tree growth resulted in the overtopping and thinning out of smaller trees, leaving regularly spaced dominants. The thinning phase continued for up to 500 years after patch initiation.

D. dacrydioides trees have small crowns and even in densely stocked stands often do not form a closed canopy (Wardle 1974). Gaps between surviving dominant trees and openings formed by the death of canopy trees were colonised by new individuals. Where there were elevated establishment sites, small openings were dominated by *W. racemosa* which formed a subcanopy tier. *P. ferruginea* and *D. cupressinum* occasionally recruited into the subcanopy or canopy. As the original canopy trees matured and then began to die further openings were formed. The beginnings of this stage of development were evident in two of the stands studied (stands K2 and F2). However, throughout the study area I could find no stands representing a further stage of development (see Oliver 1981; Peet & Christensen 1987). Similarly, Wardle (1974) could find only one stand over a more extensive region in which the mature *D. dacrydioides* canopy was beginning to open up through windfall, with the gaps filled by broadleaf species and tree ferns.

If the current patterns of patch development continue then in the absence of further major disturbance the present podocarp canopy will be replaced by a canopy dominated by broadleaf species (see also Wardle 1974; Smale 1984).

The inability of New Zealand conifer species to maintain their status in many stands has been a recurrent theme in New Zealand ecological literature (Cockayne 1928; Holloway 1954; Robbins 1962; Wardle 1963; Molloy 1969; Veblen & Stewart 1982; Ogden 1985b). Recent studies have emphasised the importance of catastrophic disturbance in initiating conifer regeneration (Veblen & Stewart 1982; Ogden 1985b; Stewart & Rose 1989). These studies conclude that postulated conifer regeneration failure (Holloway 1954; Wardle 1963) is attributable to the acceptance of classical climax theory (Clements 1916) which assumes that climax species should show within-stand self-replacement.

In the present study, major disturbance (flooding or initiation of extensive overstorey collapse) occurred frequently enough in the last 550 years to maintain the dominance of podocarps in the six stands. This is in part a consequence of the criteria I used to select stands (I chose podocarp stands that had evidence of past disturbance). However, the stands selected for study were typical of *D. dacrydioides*/*D. cupressinum* dominated stands occurring throughout the study area. Apart from trees growing on very poorly drained sites I could find no podocarp stands that lacked evidence of past disturbance. Moreover, previous studies have repeatedly emphasised the importance of disturbance in influencing forest pattern in lowland south Westland (Hutchinson 1928, 1932; Foweraker 1929; Poole 1937; Wardle 1974).

The patterns of tree establishment in the present study, in accordance with the findings of others (Six Dijkstra *et al.* 1985; B. Cornere *unpublished data*), suggest that lowland podocarp forests consist of a mosaic of relatively even-aged patches of trees that have established in response to past disturbances. The composition and structure of regenerating patches are in part determined by the type and intensity of disturbance that forms the canopy openings (see Discussion above). Vegetation change at a site may occur episodically in response to major disturbance.

The importance of historical events in influencing forest composition suggests that a model of vegetation change emphasising deterministic successional stages (eg., Wardle 1980a) may be inappropriate for these forests. For example, mixed stands of *D. dacrydioides*/*D. cupressinum* are not necessarily a stage in development from *D. dacrydioides* to *D. cupressinum* dominated forest following flooding (Wardle 1974, 1980a). These mixed stands arise because conditions suitable for the establishment of both *Dacrycarpus dacrydioides* and *Dacrydium cupressinum* are found in openings formed by both flood and wind disturbance (eg., stands F1, F2, M1 and M2).

The importance of disturbance in influencing patterns of forest regeneration suggests that a non-equilibrium model (Drury & Nisbet 1971; Pickett 1980) is appropriate for understanding the dynamics of these forests. Such a model emphasises the response of individuals to a fluctuating physical and biotic environment. Predictability in the patterns of forest succession are a consequence of predictability in gap environments and species availabilities through time. In the absence of repeated flooding, windthrow accompanied by changes in soil properties appears to favour regeneration of *D. cupressinum*, *P. ferruginea*, and *W. racemosa*.

CHAPTER VII

SUMMARY

(1). The four species studied partitioned establishment sites along gradients related to canopy cover and forest floor microrelief. Partitioning of establishment sites may contribute to the maintenance of species diversity in lowland podocarp forests. Disturbance appears critical for continued coexistence as it provided much of the environmental variation to which species differentially responded.

(2). The composition and structure of the six stands was strongly influenced by intermittent disturbance. The majority of trees in the six stands established in response to major disturbance and the forests could be described as a mosaic of relatively even-aged patches of trees.

(3). The composition and structure of regenerating patches was determined by the interaction between species regeneration requirements and the availability of suitable establishment sites. The type and intensity of disturbance and underlying environmental gradients influenced the availability of establishment sites within canopy gaps and hence subsequent forest establishment.

(4). Vegetation change at a site may occur episodically in response to periodic, major disturbance. The importance of disturbance in influencing forest composition and patterns of species turnover suggest that a non-equilibrium viewpoint, emphasising the response of individuals to a fluctuating physical and biotic environment, is appropriate for understanding the dynamics of these forests.

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APPENDIX 1: Reprint of: Duncan, R.P.; Norton, D.A.; Woolmore, C.B. 1990. The lowland vegetation pattern, south Westland, New Zealand 2. Ohinemaka Forest. New Zealand Journal of Botany **28**: 131-140.

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The lowland vegetation pattern, south Westland, New Zealand 2. Ohinemaka Forest

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Abstract The plant communities of a lowland alluvial floodplain in south Westland were classified on the basis of floristic composition from ninety eight vegetation descriptions. Five forest, one scrub, and two mire/swamp communities were identified. Plant communities were distributed in relation to landform types and soil properties. Different landforms were dominated by different plant communities and were characterised by broad soil types that reflected the nature of the landforms and the processes of soil development. Alluvial deposition and surface age were identified as important factors influencing the soil and vegetation patterns across landform types.

Keywords landform; vegetation pattern; classification; ordination; south Westland; forest; mire

INTRODUCTION

A number of studies have shown a close relationship between landform, soil, and vegetation patterns in Westland (Wardle 1977, 1980; Smith & Lee 1984; Sowden 1986; Basher 1986; Stewart & Harrison 1987a; Norton & Leathwick 1990). The distribution of soils and associated vegetation often reflects landform characteristics such as parent material, slope, drainage, stability, and surface age.

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The relationships between landforms, soils, and vegetation have been studied in the mountainous drainage basins of the Southern Alps (Basher 1986; Stewart & Harrison 1987a). The stability of landform units was found to be a major determinant of soil and vegetation patterns. Mature forest vegetation occurs on stable landforms characterised by well developed soils. Seral communities occur on well drained recent soils that are often frequently disturbed by mass movement (Stewart & Harrison 1987a).

Studies of soil sequences in lowland Westland have shown the importance of surface age in influencing soil properties (Stevens 1968; Tan 1971; Ross et al. 1977; Smith & Lee 1984; Sowden 1986). Soils on terrace sequences show a trend of decreasing available plant nutrients, increasing soil organic matter, and deteriorating drainage with increasing age. Vegetation development has been related to these changes in soil properties (Smith & Lee 1984; Sowden 1986).

Soil drainage influences vegetation pattern in Ianthe Forest, south Westland (D.A. Norton & J.A. Adams, unpublished data). Different landforms are characterised by different soil types, and drainage, which is related to slope, is a major determinant of vegetation pattern across a range of landforms. In Saltwater Ecological Area, south Westland, Norton & Leathwick (1990) related vegetation pattern to a complex of soil factors that were influenced by slope, drainage, and surface age.

Most of these studies in lowland Westland have examined the influence of one or a few factors on soil and vegetation patterns. Few studies have examined the interactions between landforms, soils, and vegetation.

South Westland contains extensive areas of low-lying, alluvial floodplains formed from post-glacial outwash debris. These surfaces support a wide range of plant communities (Wardle 1977) and their distribution has been related to broad landform types (Wardle 1980). This paper is the second in a series describing the main patterns present and the environmental factors influencing these patterns in the lowland vegetation of south Westland (see Norton & Leathwick (1990) for the first paper). The present paper describes (1) the plant communities and (2)

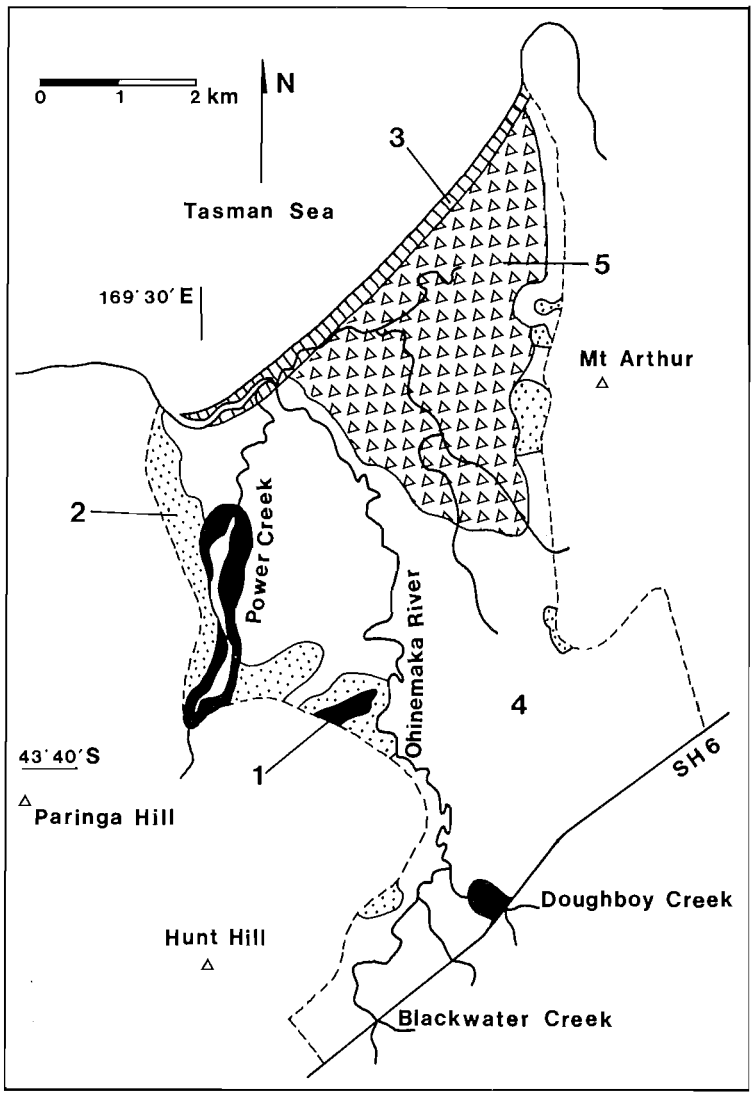

Fig. 1 Map of the study area showing the main physiographic features and the distribution of landform types. (Redrawn from Mortimer et al. 1984). The landform types are; 1. active alluvial fans; 2. stabilised alluvial fans; 3. beach deposits; 4. river gravel deposits; 5. swamp deposits. The dashed line indicates the study area boundary.

their distribution in relation to landform and soil properties, on an alluvial floodplain in Ohinemaka Forest.

STUDY AREA

The study area (3400 ha) is the flat, low-lying, post-glacial outwash surface of Ohinemaka Forest (43° 39'S, 169° 32'E) on the west coast of New Zealand's South Island. It lies between the base of Paringa Hill and Mt Arthur, bordered to the south by State Highway 6 at the base of the Douglas Range, and to the north by the Tasman Sea (Fig. 1). The area lies close to sea level with the highest points occurring around the bases of the hills (up to 60m a.s.l). Tall podocarp forest is the dominant natural cover with open mires a prominent feature in the north-east of the study area. European occupation of the region has caused some modification of the forests. Forests have been cleared for pasture in areas alongside SH6, down the Ohinemaka River and across to Power Creek. Some cleared areas have reverted back to scrub and forest, and the remaining areas of open pasture are currently grazed by cattle. Extensive cattle browsing and trampling is evident through forest and scrub adjacent to pasture and along cattle tracks. Deer sign is present throughout on drier sites.

Climate

The prevailing westerly winds and proximity to the coast result in a warm, equable climate. Mean annual precipitation at Haast (65km southwest) is 3460mm with only slight seasonal variation. Mean annual

temperature is c. 11.9°C with a January mean of 16.6°C and a July mean of 6.8°C (based on the equations of Norton 1985). Slight variations with altitude and distance from the coast are likely to occur. Ground frosts occur at Haast on an average of 37.1 days/year, mainly in the winter months (Hessell 1982).

Geomorphology

The flat topography of the study area is a result of sediment deposition following glacial retreat and subsequent erosion of the surrounding uplands. Four types of post-glacial landform are recognised in the study area (Mortimer et al. 1984).

(1) Alluvial fan and mass movement deposits. These are further subdivided into (a) active alluvial fans, currently active or with deposition occurring in the last 25 years (b) stabilised alluvial fans or mass movement deposits covered with vegetation.
(2) River gravel deposits, mainly sand and gravel. These deposits have a well developed vegetative cover and are unlikely to be older than about 6000 years. Similar deposits in the adjacent Mahitahi Catchment have been estimated at 6000–3000 years old, although elsewhere they may be somewhat younger (Mortimer et al. 1984).
(3) Beach deposits of sand immediately east of the present coastline.
(4) Swamp deposits composed largely of peat and mud, and probably underlain by river gravel deposits (Mortimer et al. 1984). These deposits are less than 5000 years old. The sea level stabilised at its present height about 6000 years BP and 5000 years BP the coastline was some 3km inland of its present position (Mortimer et al. 1984). Subsequent sediment deposition caused retreat of the coastline and the swamp deposits were formed in an area that was evidently an old lagoon (Wardle 1979).

METHODS

The study area was sampled during the 1984/85 summer. Sampling sites were located at 457m (500 yard) intervals along east–west transects 914m (1000 yard) apart, based on the NZMS 1, S78 mapping grid. Additional sites were located where pronounced vegetation changes were encountered along transects.

Vegetation data were collected in unbounded plots using a variation of the method of Allen & McLennan (1983). At each plot up to six physiognomic strata of variable height [as opposed to fixed heights in Allen & McLennan (1983)] were recognis-ed and the mean height of each stratum estimated. In each stratum all vascular species present were recorded and assigned to cover classes (<1, 1–5, 6–25, 26–50, 51–75, and 76–100%) based on their percentage cover in that stratum. Altitude and soil depth were measured at each plot and soil drainage was assessed as either good, medium, or poor. Ninety eight plots in uncleared vegetation were sampled.

Simultaneous classification of plots and species based on floristic composition (i.e., species presence/absence) was performed using indicator species analysis (ISA: Hill et al. 1975) as implemented in TWINSPAN (Hill 1979a). Divisions were individually examined and groups accepted at various levels depending upon their interpretability. Communities were named using the method of Atkinson (1985) with the following modifications;
no brackets around species indicate >10% cover
( ) brackets indicate 5–10% cover
[ ] brackets indicate <5% cover
the term forest is used to describe communities where trees are physiognomically dominant over shrubs.

To assist community description and the interpretation of vegetation patterns "constant" species were defined as those with a frequency of >80% in any one community, and "indicator" species were obtained from the ISA output.

Indirect ordination of plots and species based on floristic composition was performed using detrended correspondence analysis (DCA: Hill & Gauch 1980) as implemented in the program DECORANA (Hill 1979b). This technique produces axes summarising floristic change. Oblique rotational correlation analysis (Dargie 1984; Bowman & Minchin 1987) using Spearman's rank correlation coefficients was used to compare the ordination output with environmental variables using STATISTIX (NH Analytical Software 1987, 1958 Eldridge Avenue, Roseville, MN 55113).

RESULTS

Plant communities

Eight communities were recognised from the ISA output (Fig. 2). The mean percentage cover, summed over all tiers, of 43 "constant" and "indicator" species are used to summarise the main vegetation differences between the communities (Table 1). A brief description of the communities follows with comparable communities in Wardle (1977) indicated in square brackets [ ].

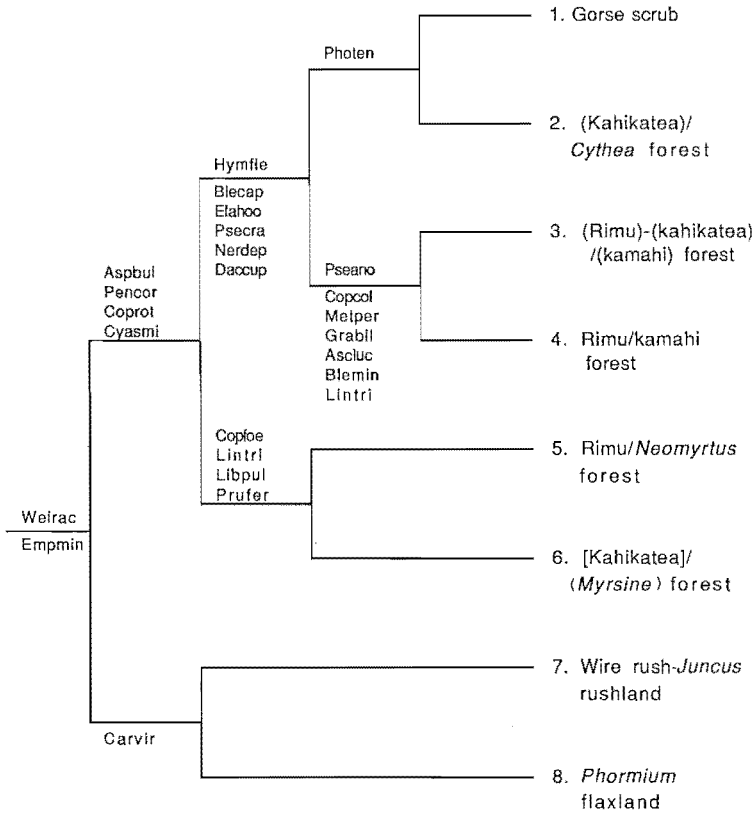

Fig. 2 Dendrogram of ISA output showing the relationships between the eight communities, and the indicator species identified at each division. Species codes are the first three letters of the generic and specific name for each species. Full names are given in Table 1.

1. Gorse scrub (2 plots).
Gorse (*Ulex europaeus* L.*) dominates this community forming a dense cover 1–1.5 m tall with *Phormium tenax* and *Ascarina lucida* locally dominant. *Histiopteris incisa* is locally dense on the ground. [Coastal *Phormium tenax* and gorse scrub, N3].

2. (Kahikatea)/*Cyathea* forest (15 plots).
Stands in this community are structurally variable ranging from a diverse canopy of broadleaved species to scattered emergent kahikatea (*Dacrycarpus dacrydioides*) and matai (*Prumnopitys taxifolia*) over a kamahi (*Weinmannia racemosa*)/*Cyathea smithii* canopy to stands of tall, dense kahikatea. The density of broadleaved canopy and shrub species varies with podocarp density and the forest is open under tall, dense kahikatea. [Kahikatea forest, A1a; Kahikatea/hardwood forest, B2a; Low forest on lowland river flats, D1a].

3. (Rimu)-(kahikatea)/(kamahi) forest (19 plots).
Kahikatea and rimu (*Dacrydium cupressinum*) form a mixed canopy with rimu usually dominant. Kamahi and miro (*Prumnopitys ferruginea*) form a prominent subcanopy. [Rimu-kahikatea forest, A2b].

4. Rimu/kamahi forest (14 plots).
Rimu forms a closed canopy with kahikatea occurring in the emergent or canopy strata in eight of the plots. Kamahi and miro form a prominent subcanopy. Windfall was noted in 43% of the plots. [Rimu forest, A2a].

5. Rimu/*Neomyrtus* forest (19 plots).
Rimu forms a closed canopy with occasional southern rata (*Metrosideros umbellata*). Below this kamahi forms an open subcanopy with miro and occasional Hall's totara (*Podocarpus hallii*). The shrub stratum is dense and dominated by *Neomyrtus pedunculata* with *Phyllocladus alpinus* locally common. In three plots silver pine (*Lagarostrobos colensoi*) co-dominates with rimu forming a lower canopy. [Rimu forest, A2a; Rimu-silver pine forest, A2c].

6. [Kahikatea]/(*Myrsine*) forest (16 plots).
Kahikatea with occasional silver pine and rimu occurs over a dense shrub stratum dominated by *Myrsine divaricata*. *Carex* species are locally common in the ground stratum. [Open kahikatea forest transitional to swamps, B1].

*Nomenclature follows Allan (1961), Moore & Edgar (1970), Brownsey et al. (1985), and recent taxonomic changes listed in Connor & Edgar (1987) unless otherwise indicated.

7. Wire rush-*Juncus* rushland (12 plots).
Empodisma minus, *Juncus gregiflorus*, and *Gleichenia dicarpa* (9 plots) form a low, dense sward with stunted manuka occurring in patches, occasionally forming a scrub canopy. [Lowland infertile swamp, K2].

Table 1 Mean percentage cover of the constant and indicator species in each of the eight communities. + indicates a mean cover of <1%. Boxes around numbers indicate a >80% frequency in that community. Community names are given in the text.

	Community							
Species	1	2	3	4	5	6	7	8
Ulex europaeus	71		+			+		
Histiopteris incisa	19	+	+	+	+			
Phymatosorus diversifolius	+	+	+	+		+		
Phormium tenax	2		+		+	2	+	38
Coprosma rotundifolia		9	1	+				
Cyathea smithii	2	16	6	4	+	+		
Pennantia corymbosa		7	1	+				
Asplenium bulbiferum		2	1	+	+	+		
Dacrycarpus dacrydioides		6	5	4	2	4	+	
Dicksonia squarrosa	+	9	6	5	+	+		
Microlaena avenacea	+	8	4	4	+	2		
Weinmannia racemosa		10	9	14	8	3		
Coprosma ciliata	+	3	2	+	+	1		
Hedycarya arborea	1	3	2	+	+	+		
Coprosma rhamnoides		1	4	3	+	2		
Metrosideros diffusa		2	3	+	+	+		
Nertera depressa	+	1	4	+	+	1		
Nertera dichondrifolia	+	2	1	1	+	+		
Pseudowintera colorata		5	6	3	+	1		
Prumnopitys ferruginea		+	4	4	3	+		
Dacrydium cupressinum		+	7	13	13	1		
Ascarina lucida	4	+	2	3	2	1		
Ripogonum scandens	+	+	+	+	+	+		
Neomyrtus pedunculata		1	6	5	16	2		
Pseudopanax crassifolius	+	+	1	2	2	1	+	
Coprosma foetidissima		+	+	+	1	+		
Hymenophyllum flexuosum	+							
Metrosideros perforata				+	+			
Lindsaea trichomanoides				+	+			
Libertia pulchella				+	+			
Pseudopanax anomalus		+	1	+	+	+		
Blechnum minus			+	+	1	+		
Grammitis billardierei			+	+	+	+		
Elaeocarpus hookerianus			1	1	1	+		
Coprosma colensoi				+	1	2	+	
Astelia grandis		1	+	+	+	5		
Blechnum sp.*			1	1	+	3	+	4
Griselinia littoralis		+	2	2	1	1	+	
Myrsine divaricata		+	2	2	1	8		
Leptospermum scoparium				+	2	6	5	4
Empodisma minus					+		24	
Juncus gregiflorus	+				+	1	13	
Carex virgata						+		+

**B. capense* sensu Allan (1961).

8. *Phormium* flaxland (1 plot).
Phormium tenax up to 3m tall dominates this community with manuka, *Coprosma* aff. *parviflora* and *C. propinqua* common in the shrub tiers. *Astelia grandis*, *Blechnum sp.* cf. *B. capense* and *Carex* species are locally common. [Lowland fertile swamp, K1].

Factors influencing the vegetation pattern

Altitude showed no significant correlation with plot axes on the ordination diagram (Table 2) and no clear differences between the community types, reflecting the small range in altitude (60m) across the study area.

Plant communities are distributed in relation to different landforms (Fig. 3a) and occur on sites that differ in drainage and soil depth (Fig. 3b, c). Landform and soils appear closely related, with soil properties reflecting the nature of the landform and the processes of soil development. The distribution of plant communities is related to landforms that are characterised by broad soil types differing in drainage and soil depth.

Gorse scrub occurs as a narrow strip on beach deposits immediately east of the present coastline (Fig. 1, 4), on well drained, shallow soils formed on sand. (Kahikatea)/*Cyathea* forest dominates the area between the Ohinemaka River and the base of the Paringa Hills on recent, well drained soils derived from river gravel and alluvial deposits. The area has been subject to alluvial deposition in the region of Power Creek and along the base of the Paringa Hills, and the surface between the Paringa Hills and the Ohinemaka River has been formed relatively recently as a result of outwash deposition from the Paringa Hills. The southern part of the study area along Blackwater Creek and SH6, at the base of the Douglas Range is dominated by (rimu)-(kahikatea)/(kamahi) forest occurring predominantly on moderately to

Table 2 Relationships between DCA plot scores and measured environmental variables.

Spearman rank correlation coefficients comparing axis 1 and 2 of the DCA output with measured environmental variables.

	Drainage	Soil depth	Altitude
Axis 1	0.577	0.534	–0.346
Axis 2	0.138	0.273	–0.148

Oblique rotational correlation analysis showing the maximum Spearman rank correlation coefficients obtained using both axes [axis1 + k(axis2)].

Drainage	k=0.6	r=0.589
Soil depth	k=1.1	r=0.650

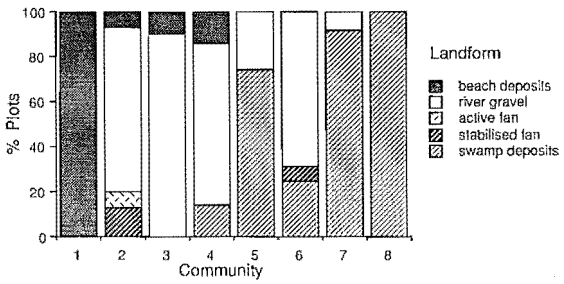

Fig. 3a The percentage of plots on different landform types in the eight plant communities. Community names are given in the text.

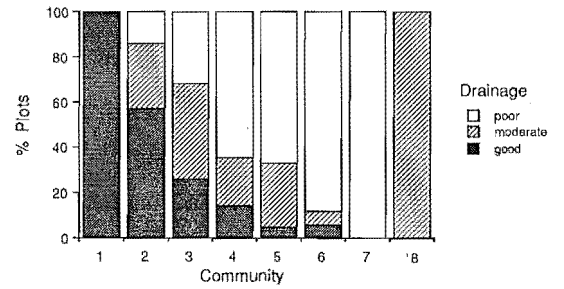

Fig. 3b The percentage of plots in three drainage classes in the eight plant communities. Community names are given in the text.

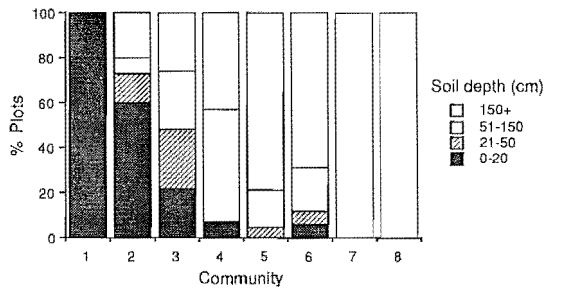

Fig. 3c The percentage of plots in four soil depth classes in the eight plant communities. Community names are given in the text.

well drained soils derived from river gravel and alluvium. Recent alluvial deposits are evident around Doughboy Creek and older deposits around the base of Hunt Hill.

The Ohinemaka River forms a distinct soil and vegetation boundary. Outwash from the Paringa Hills would be carried to the coast on reaching the river and, apart from floodbank deposits, does not extend further east. Soils in the northern half between the Ohinemaka River and Mt Arthur are predominantly poorly drained, deep soils on swamp deposits and dominated by wire rush-*Juncus* rushland and rimu/*Neomyrtus* forest. The southern edge of the swamp deposits is marked by a change in vegetation with rimu/kamahi forest dominating in the central region between the Ohinemaka River and Mt Arthur, on poorly drained, moderately deep soils formed on river gravel deposits.

Phormium flaxland occurs alongside open water or in wet depressions where fertility is maintained by water movement and periodic deposition of alluvium. This community is found throughout the study area and is prominent in the south along the base of the Douglas Range. [Kahikatea]/(*Myrsine*) forest occupies similar sites often forming a forest margin around *Phormium* flaxland communities. It is scattered throughout the study area on poorly drained sites.

The close relationship between soil properties and vegetation pattern is reflected in the significant correlations between drainage, soil depth, and plot position on the ordination axes (Table 2). The gradient of maximum correlation runs from the bottom left to the top right of the ordination diagram (Fig. 5) and changes in community composition parallel changes along the drainage and soil depth gradients. Plant communities that occupy well drained, shallow soils (gorse scrub and (kahikatea)/*Cyathea* forest) are at the bottom left of the ordination diagram. Moving up and to the right along the gradients of deteriorating drainage and increasing soil depth, rimu becomes dominant over kahikatea with silver pine and rimu dominating in forest plots in the upper right of the ordination diagram.

Although changes in community composition and species cover along the environmental gradients are apparent, some species show a consistent relationship to site conditions. Species characteristic of well drained, shallow soils such as *Coprosma rotundifolia*, *Pennantia corymbosa*, and *Cyathea smithii* are at the bottom left of the species ordination (Fig. 6) while those characteristic of poorly drained, deep soils such as *Empodisma minus*, *Blechnum minus*, and *Libertia pulchella* are at the upper right of the ordination. Species with intermediate positions are characteristic of a range of sites and include rimu, kahikatea, and kamahi.

DISCUSSION

In the study area landform, soils, and vegetation are closely related. Soil and vegetation patterns in part

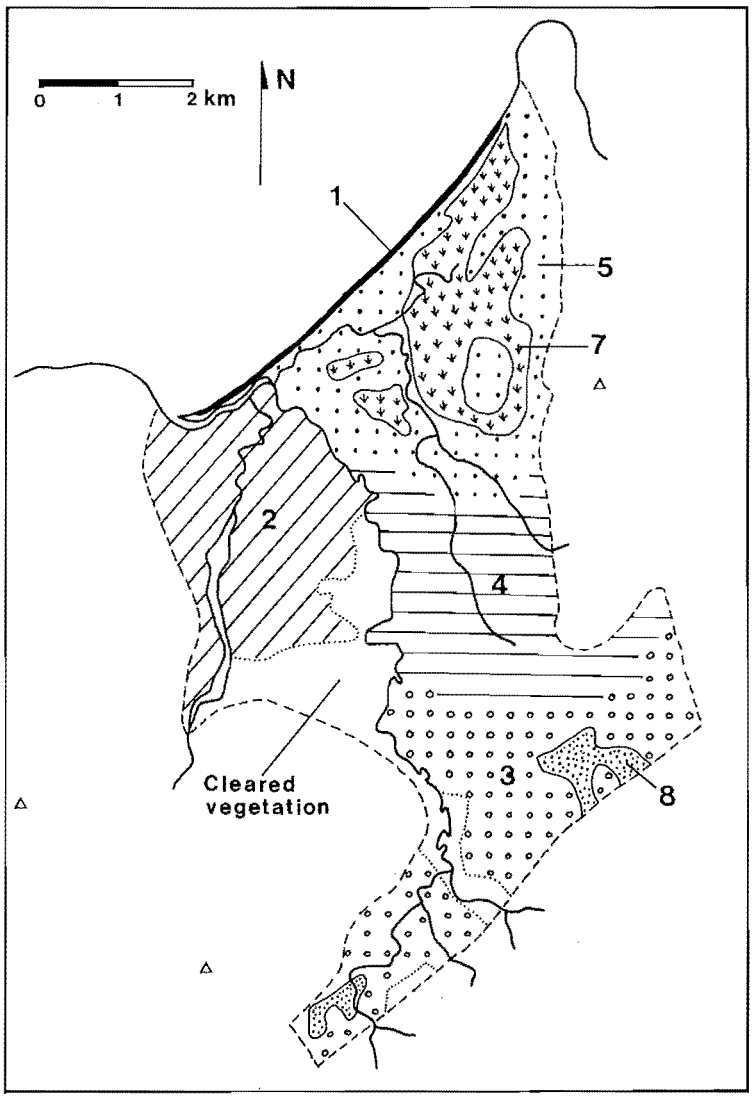

Fig. 4 Vegetation map of the study area. Community 6, [kahikatea]/(*Myrsine*) forest, is not mapped because it is dispersed throughout. Mapping was based on plot data, aerial photographs, and ground checks. The mapped communities are; 1. gorse scrub; 2. (kahikatea)/*Cyathea* forest; 3. (rimu)-(kahikatea)/(kamahi) forest; 4. rimu/kamahi forest; 5. rimu/*Neomyrtus* forest; 7. wire rush-*Juncus* rushland; 8. *Phormium* flaxland.

reflect the influence of landform stability and surface age. Sites with the youngest deposits of alluvium are characterised by well drained, shallow soils and dominated by (kahikatea)/*Cyathea* forest. In the south of the study area moderately drained soils supporting (rimu)-(kahikatea)/(kamahi) forest may reflect longer periods of soil development in the absence of major deposition. The areas least affected by recent deposits of alluvium are in the north between the Ohinemaka River and Mt Arthur. In the central region poorly drained, moderately deep soils have formed on river gravels, reflecting longer periods of soil development on a stable surface. The susceptibility of different parts of the study area to alluvial deposition is influenced by the surrounding upland geology and patterns of drainage. Recent sediment deposition around Power Creek and the base of the Paringa Hills is derived from Palaeozoic greywackes which are very susceptible to mass wasting and gullying (Fitzsimons & O'Loughlin 1984). In contrast the Cretaceous sedimentary rocks and moraine deposits of Mt Arthur, and the Palaeozoic granites of Hunt Hill are relatively stable (Fitzsimons & O'Loughlin 1984) with little erosion and outwash deposition.

Mass movement on unstable landforms has an important influence on soil properties and results in similar patterns in the mountainous drainage basins of the Southern Alps (Stewart & Harrison 1987a,b; Basher 1986). Unstable landforms subject to deposition are characterised by recent, fertile soils. On stable landforms where soil development has

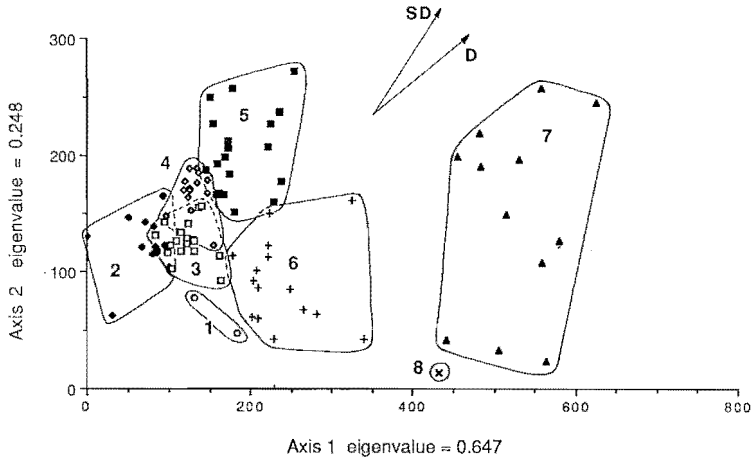

Fig. 5 Scatter diagram of axis 1 and axis 2 of the plot ordination obtained from the DCA output, with ISA communities superimposed. Community names are given in the text. The two arrows show the directions of maximum correlations of drainage, D, (r=0.589) and soil depth, SD, (r=0.650) with plot positions on the two ordination axes.

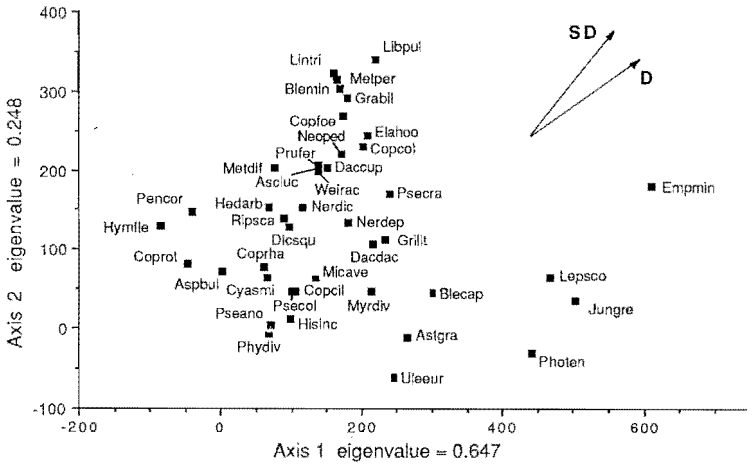

Fig. 6 Scatter diagram of axis 1 and axis 2 of the species ordination obtained from the DCA output. Only constant and indicator species from Table 1 are plotted. Species codes are the first three letters of the generic and specific name for each species. Full names are given in Table 1. The two arrows show the directions of maximum correlations of drainage, D, (r=0.589) and soil depth, SD, (r=0.650) with plot positions on the two ordination axes.

proceeded unaffected by disturbance for longer periods soils are poorly drained and infertile (Stewart & Harrison 1987b). A trend of deteriorating drainage and increasing soil depth occurs with increasing age on lowland forested terrace sequences in South Westland (Smith & Lee 1984; Sowden 1986) and a similar pattern of vegetation and soil change associated with increasing surface age has been described on the alluvial flats around Westland National Park, to the north of the study area (Wardle 1980) and in Saltwater Ecological Area (Norton & Leathwick 1990). Changes in forest canopy dominance from kahikatea to rimu are thought to reflect decreasing soil fertility associated with podzolisation and gleying (Wardle 1974).

Soil characteristics such as poor drainage can arise as a result of factors other than soil age (Smith & Lee 1984). Swamp deposits were formed within the last 5000 years as a result of sediment deposition and retreat of the coastline. They occupy the old lagoon area with a low-lying topography and impeded drainage resulting in a high water table. Accumulation of mud and organic matter under these waterlogged conditions has created deep, poorly drained soils. The distribution of mire and forest communities on this surface may be relatively stable and determined by environmental gradients. A change from forest to open mire has been shown to parallel an increase in soil depth on similar sites to the north of the study area (Norton 1989).

Whereas the broad vegetation patterns can be related to landform and soil patterns, the factors controlling vegetation distribution can only be inferred from the limited environmental data. Soil

depth, drainage, fertility, landform age, and past physical disturbance have been indicated as related factors influencing vegetation distribution. Further detailed investigation is required to determine the relative importance of these factors, and some of these may account for much of the smaller scale variation throughout the area.

ACKNOWLEDGMENTS

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APPENDIX 2: Reprint of: Duncan, R.P. 1989. An evaluation of errors in tree age estimates based on increment cores in kahikatea (*Dacrycarpus dacrydioides*). New Zealand Natural Sciences **16**: 31-37.

AN EVALUATION OF ERRORS IN TREE AGE ESTIMATES BASED ON INCREMENT CORES IN KAHIKATEA (*DACRYCARPUS DACRYDIOIDES*).

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ABSTRACT

Duncan, R.P. (1989). An evaluation of errors in tree age estimates based on increment cores in kahikatea (*Dacrycarpus dacrydioides*). *New Zealand Natural Sciences* 16: 31-37.

Twelve kahikatea (*Dacrycarpus dacrydioides*) discs were used to assess the likely errors associated with estimating tree age from growth ring counts in increment cores. Two major sources of error were examined: (1) Failure of the increment core to pass through the tree's chronological centre. A geometric model is developed for estimating the distance to the chronological centre in cores where the arcs of the inner rings are visible. The mean percentage error from 84 cores that passed within 50 mm of the chronological centre was ±35% corresponding to a mean absolute error of ±21 years. The majority of this error is due to growth rate differences between the missing radius and the measured part of the core. (2) Missing rings. The average age underestimate from 48 cores due to missing rings was 13%. A significant correlation between radius length and age under estimate (r = 0.81) suggests that sampling along the longest radii will reduce this error. The average age underestimate due to missing rings from cores located along the longest radii of the twelve samples was 3%.

KEYWORDS: *Dacrycarpus dacrydioides* - kahikatea - dendroecology - tree age estimate - growth ring - dendrochronology.

INTRODUCTION

Tree-ring counts from increment cores are widely used in ecological studies as a non-destructive means of estimating tree ages. Three problems arise when using growth rings from increment cores to estimate tree age (Norton *et al.* 1987):

1. For a variety of reasons increment cores often fail to reach the chronological centre of the tree, and age must be extrapolated for the missing portion of the radius (see Norton *et al.* (1987) for terminology).
2. Missing rings are common in many New Zealand trees with frequent "wedging out" of groups of rings along some radii (i.e. growth rings are absent around a portion of the circumference).
3. Sampling is rarely at ground level, and the time taken by the tree to reach the sampling height has to be estimated.

By examining kahikatea (*Dacrycarpus dacrydioides*) discs of known age this paper investigates the first two of these problems.

Estimation of the age of the missing radius involves three steps:

1. Estimating the position of the chronological centre, and obtaining an estimate of the length of the missing radius.
2. Estimating the mean ring width in the missing radius.
3. Dividing the estimated length by the estimated mean ring width to obtain an estimate of age in the missing radius.

The tree's geometric centre is often used as an estimate of the position of the chronological centre in order to obtain the length of the missing radius (Wardle 1963, Clayton-Greene 1977, Allen 1988). A previous study (Norton *et al.* 1987) has investigated the errors associated with this method in 4 New Zealand tree species (*Agathis australis, Libocedrus bidwillii, Nothofagus solandri,* and

Prumnopitys taxifolia). In the present study a geometric model is developed for estimating the length of the missing radius in cores where the arcs of the inner growth rings are visible (Fig. 1). The errors associated with the application of this model to kahikatea trees are investigated.

Missing rings due to ring wedging have been identified in a number of New Zealand tree species (Dunwiddie 1979, Norton *et al.* 1987) and are thought to be a result of the development and death of major branches, and consequent variations in food and growth regulator supplies (Fritts *et al.* 1965). A number of authors have commented on the difficulties in ageing discs of species that exhibit a high rate of ring wedging often associated with irregular or lobate diameter growth (Dunwiddie 1979, Norton *et al.* 1987, Norton & Ogden 1987). Errors in age estimates are likely to be accentuated if based on increment cores, since missing rings on single radii can be as high as 10% of the total number of rings present (Norton & Ogden 1987). The present study investigates the likely errors caused by missing rings in increment cores from kahikatea trees.

A GEOMETRIC MODEL FOR ESTIMATING THE MISSING RADIUS

Increment cores often pass close enough to the chronological centre that the arcs of the inner rings are visible. Applequist (1958) used a device called a "pith locator" to estimate the distance to the chronological centre based on the curvature of these inner rings. Norton *et al.* (1987) suggest a similar method of tracing the arcs, fitting circles to them using a compass, and then measuring the length of the missing radius. Alternatively the length of the missing radius (r) can be related to the height (h) and length (L) of an arc (Fig. 1) by Equation 1:

$$r = \frac{L^2}{8h} + \frac{h}{2}$$

Equation 1.

This model assumes concentric growth from the chronological centre to the increment core. Dunwiddie (1979) notes that lobate growth in young trees of kahikatea is not excessive, and growth close to the chronological centre may be approximately concentric. For cores passing close to the centre this assumption may therefore be valid.

Liu (1986) proposed a similar model for estimating the lengths of missing radii based on measurements of growth rings at the tree circumference and the diameter of the increment core. Liu's (1986) model assumes concentric growth for the entire age of the tree, an assumption which appears invalid for most New Zealand tree species (Norton *et al.* 1987).

MATERIALS AND METHODS

APPLICABILITY OF THE GEOMETRIC MODEL

Discs from the bases of twelve kahikatea trees were sanded using successively finer grades of sandpaper until the growth rings were clearly visible. Seven lines representing theoretical increment cores were drawn on each disc. The lines were drawn from randomly located points on the disc's circumference to points 5, 10, 15, 20, 30, 40 and 50 mm from the tree's chronological centre (distance m in Fig. 1). A second line, parallel to the first, was drawn at a further 5 mm from the tree's chronological centre (the diameter of commercially available increment cores). These lines represent increment cores that have missed the chronological centre by 5, 10, 15, 20, 30, 40 and 50 mm respectively. Unless stated otherwise all lengths were measured to ±0.1 mm using vernier callipers. Lengths less than 30 mm were measured, and growth rings counted under reflected light using 0.6x binocular magnification. Growth ring formation was assumed to be annual.

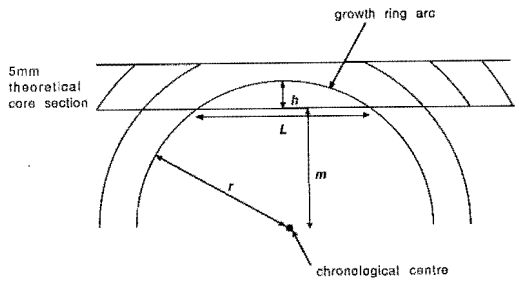

Figure 1. Diagram of a theoretical core section showing the height (h) and length (L) of an inner growth ring arc, the missing radius (r), and the distance by which the core misses the chronological centre (m).

In all cases more than one arc was visible in the 5 mm section representing the increment core. The arc selected for measurement was chosen using the following guidelines (in order of precedence):

1. The arc was free of any ring wedging within the 5 mm core section.

2. The arc was the largest visible in the 5 mm core section. This minimises the error in deriving the estimated missing radius due to measurement errors in h and L.

The lengths h, L and the true length of the missing radius were measured and an estimate of the length of the missing radius was derived using Equation 1.

The number of rings in the missing radius were counted and the mean ring width determined. The mean ring widths of the innermost 20 and 50 growth rings in each theoretical core (starting from the measured arc) were used as estimates of mean ring width in the missing radius (cf. Norton *et al.* 1987). The lengths used for the calculation of mean ring widths (d in Fig. 2) were corrected to compensate for the offsetting of the theoretical core from the tree centre using Equation 2:

$$d_{\text{corrected}} = \sqrt{\left(\frac{L^2}{8h} - \frac{h}{2}\right)^2 + \left(d + \frac{L}{2}\right)^2} - \left(\frac{L^2}{8h} + \frac{h}{2}\right)$$

Equation 2.

Estimates of the number of growth rings in the missing radius were obtained by dividing the estimated length of the missing radius by the mean ring widths obtained from the 20 or 50 innermost growth rings.

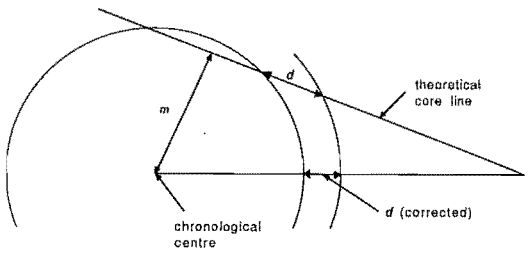

Figure 2. Diagram of an off-set core showing the measured (d) and the corrected ($d_{\text{corrected}}$) distances used for calculating mean ring width, and the distance by which the core misses the chronological centre (m).

ESTIMATION OF MISSING RINGS

The high degree of ring wedging and lobate growth in the twelve sampled discs made accurate determination of the true age difficult. An estimate of the true age of each disc was obtained by counting rings along a radius from the chronological centre. When it was apparent that the radius was missing rings, a growth ring circumference was followed around until counting could be continued on another radius that included the missing rings. This procedure was continued to the disc circumference thus giving an estimate of the true age.

Four locations, representing increment core sampling points were subjectively located on the circumference of each of the sanded discs. The points were located in an attempt to simulate likely field sampling positions using the following guidelines:

1. All of the discs exhibited lobate growth, often with deep fluting, giving an irregular circumference. Points were located on the ends of the largest lobes.

2. An attempt was made to place one point in each quarter of the circumference (this was not always practical).

Lines representing theoretical increment cores were drawn from the chronological centre to the four points on the disc's circumference. In all cases the longest radius was included as a theoretical core. The growth rings along each line were counted under reflected light using 0.6x magnification, and the core's length was measured to ±1 mm using a steel ruler.

RESULTS

APPLICABILITY OF THE GEOMETRIC MODEL

Comparisons between the estimated and true missing radius length, mean ring width and age of the missing radius were made in three ways (cf. Norton *et al.* 1987): (1) the absolute differences between estimated and true values were determined and the values averaged to give a mean for each method; (2) the absolute differences were expressed as a percentage error of the true value and averaged to give a mean percentage error for each method; (3) the number of over- and under-estimates were tallied for each method, and significant deviations from expected frequencies were determined using a Chi-square test. In some age

estimates the estimated age equalled exactly the true age; the error of ±0% was added into the average of the class but the core is not represented as either an over- or under-estimate in the tables.

Results from the estimation of the missing radii lengths are summarised in Table 1. The mean percentage error from all cores is ±21% and individual errors ranged from -40.5 to 111.5%. The absolute error increased with increasing distance from the chronological centre. Some of the error in the estimated radius length is due to measurement error in the lengths h and L. In all estimates h was >2 mm and L was >10 mm. With a measurement accuracy of ±0.1 mm the maximum error in the estimated radius due to measurement errors in h and L is less than 7% (unpub. data). Larger errors occur as a result of non-concentric growth. There was no significant trend to over- or under-estimate missing radius length.

Results from the estimation of mean ring widths are summarised in Table 2. The method of estimating mean ring width appears to make little difference, since the mean percentage errors of the 20 and 50 innermost ring estimates are 43 and 47% respectively. The ranges of individual errors for the two methods are -52.0 to 213.4% and -53.6 to 268.6% respectively. Errors due to measurement and the assumption of concentric growth in deriving the corrected lengths are likely to be small. The majority of error is caused by differences between the actual growth rates in the missing radius and the actual growth rate in the measured part of the core. Significantly more mean ring widths were over-estimated ($P < 0.05$). In most cases the discs showed suppressed early growth, with narrow rings followed by growth release. The 20 and 50 innermost rings often occurred within the period of release resulting in an overestimate of mean ring width.

The results of estimation of missing radii age are summarised in Table 3 for the two methods of mean ring width estimation. The absolute error in age estimate tends to be smaller in cores that pass closer to the chronological centre. Significantly more ages were under-estimated ($P < 0.05$) as a result of the tendency to over-estimate mean ring width.

Estimation of missing rings

The true age of the sampled discs ranged from 390 to 555 years with a mean of 455 years. The difference between the number of growth rings counted along each of the four core lines and the samples true age was expressed as a percentage under-estimate of the true age. For each sample the lengths of the core lines were expressed as a percentage of the longest radius of the sample. Core length expressed as a percentage of the longest radius was plotted against percentage age under-estimate (Fig. 3) and the two were found to be significantly correlated ($r = 0.81, n = 48$). For a given sample, cores measured on longer radii

Distance from chronological centre (mm).	Mean absolute error ± S D (mm).	Mean percentage error ± S D	Number of over/under estimates.
5	1.4 ± 0.9	15.9 ± 9.6	7/5
10	2.9 ± 3.5	19.7 ± 23.3	6/6
15	3.6 ± 2.7	19.4 ± 14.9	6/6
20	4.0 ± 3.2	16.4 ± 13.3	3/9
30	6.2 ± 4.1	18.3 ± 11.3	7/5
40	13.7 ± 17.3	30.5 ± 36.5	5/7
50	14.0 ± 7.2	25.8 ± 12.5	3/9
	6.5 ± 8.7	20.8 ± 20.1	37/47 ($X^2 = 1.19, P < 0.5$)

Table 1. Summary of the results of estimation of the missing radius length.

	Mean ring width ± S D (mm).	Mean percentage error ± S D.	Number of over/under estimates.
Missing radius	0.540 ± 0.177		
20 inner rings	0.651 ± 0.282	43.3 ± 45.8	53/31 ($X^2 = 5.76, P < 0.05$)
50 inner rings	0.669 ± 0.268	47.4 ± 56.7	61/23 ($X^2 = 17.19, P < 0.01$)

Table 2. Summary of the results of estimation of mean ring width.

tend to give better estimates of true age. The mean age under-estimate of all cores was 13.3 ± 9.6%, while the mean age under-estimate of the longest radius in each sample was 3.4 ± 2.2%. The largest individual age underestimate due to missing rings was 39.5%.

DISCUSSION

This method of estimating the age of the missing radius has a mean percentage error of ±35%. This represents a ±21 year age estimate error. For the sampled discs with a mean age of 455

Distance from chronological centre (mm).	Mean absolute error ± S D (years).	Mean percentage error ± S D	Number of over/under estimates.
20 INNER RINGS			
5	5.3 ± 3.7	30.1 ± 23.5	6/5
10	8.1 ± 8.8	21.8 ± 12.8	4/7
15	13.9 ± 11.9	32.3 ± 23.9	5/7
20	16.0 ± 8.3	32.2 ± 13.5	3/9
30	21.6 ± 15.9	33.6 ± 21.3	2/9
40	45.8 ± 56.4	58.9 ± 83.8	4/8
50	37.4 ± 23.7	41.2 ± 25.6	4/8
	21.2 ± 27.7	35.4 ± 37.4	28/53 ($X^2 = 6.37, P < 0.05$)
50 INNER RINGS			
5	6.8 ± 5.0	34.8 ± 20.6	6/6
10	7.3 ± 9.5	18.1 ± 16.2	2/10
15	10.3 ± 13.8	21.1 ± 20.8	2/10
20	15.7 ± 13.3	28.9 ± 20.4	4/8
30	20.4 ± 15.4	30.1 ± 21.9	2/10
40	54.2 ± 66.1	67.6 ± 95.9	5/7
50	37.3 ± 31.8	41.8 ± 39.9	5/7
	21.7 ± 32.9	34.6 ± 43.7	26/58 ($X^2 = 12.19, P < 0.01$)

Table 3. Summary of the results of estimation of missing radii age.

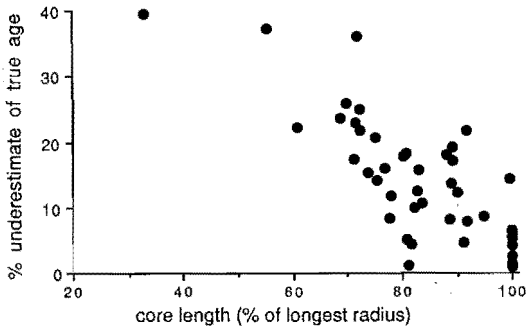

Figure 3. Plot of core length (expressed as a percentage of the longest radius) against core age (expressed as a percentage underestimate of true age) for 48 theoretical cores. $r = 0.81$.

years this represents an error of ±5% in the total age estimate.

Comparisons with the method of Norton *et al.* (1987) who used the geometric centre are difficult, as the errors in that study are given only as a percentage of total tree age. Average tree ages are not given, making it impossible to derive a comparative measure of the error in missing radius estimate independent of the tree age. The two methods also differ in their application. The geometric centre is used as an estimate of the position of the chronological centre when an increment core fails to reach the centre, because the corer is too short or because of a rotten tree centre (e.g., Clayton-Greene 1977, Allen 1988). When an increment core passes to the side of the chronological centre and the inner growth rings arcs are visible these can be used to estimate the position of the chronological centre (Applequist 1958, Clayton-Greene 1977, Norton *et al.* 1987). It would be expected that this latter method would provide better estimates of missing radius length, since the position of the chronological centre is estimated from direct evidence (the inner growth ring arcs) rather than the assumption that it is located at the geometric centre. The majority of error in the estimation of the length of the missing radius (Table 1) is due to non-concentric growth close to the tree centre. Other tree species will vary in this respect. Eccentric or lobate growth when trees are young is likely to increase the errors in age estimates.

On average the majority of the error in age estimates was due to error in the estimation of mean ring width in the missing radius. In the sampled discs there was a tendency to over-estimate mean ring width and so under-estimate age, due to a period of suppressed early growth. In trees that show a period of rapid initial growth followed by suppression, the tendency will be to over-estimate age. In general the sign of this error is unpredictable (Norton *et al.* 1987) and depends on individual tree growth patterns, the distance of the core from the tree centre, and the portion of the core used for ring width estimation.

The errors in age estimates (Table 3) ignore the effects of missing rings. In cores where rings are missing due to ring wedging age will be underestimated. This is the case even when a core passes through the chronological centre. The mean error in age estimates due to missing rings was 13%. However, by taking four increment cores and using only the core with the greatest number of growth rings, the mean under-estimate in the true age of the samples is reduced to 3%. The significant correlation between radius length and error in age estimate in the kahikatea samples suggests that field sampling along the longest radii will reduce errors due to missing rings.

The total error in age estimates based on increment cores is due to a combination of errors associated with estimating age in the missing radius and errors associated with missing rings. By combining the two values the results suggest that in the sampled discs the average error in age estimate in cores measured along the longest radius, and passing within 50 mm of the tree's chronological centre is less than 10%.

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APPENDIX 3: Formulae for the variance of Moran's *I* coefficient under the null hypothesis of randomization.

The variance of *I(d)* under the null hypothesis of randomization is given by:
(see Cliff & Ord 1981, p. 21, equation 1.39; Upton & Fingleton 1985, p. 171, equation 3.29)

$$var[I(d)] = \frac{N[(N^2-3N+3)S_1 - NS_2 + 3S_0^2] - k[N(N-1)S_1 - 2NS_2 + 6S_0^2]}{(N-1)^{(3)} S_0^2}$$

$$- \frac{1}{(N-1)^2}$$

Where:

$$S_0 = \sum_i \sum_j w_{ij} \; ; \qquad (i \neq j)$$

$$S_1 = \frac{1}{2} \sum_i \sum_j (w_{ij} + w_{ji})^2 \; ; \qquad (i \neq j)$$

$$S_2 = \sum_i (w_{io} + w_{oi})^2$$

$$w_{io} = \sum_j w_{ij} \qquad w_{oi} = \sum_j w_{ji}$$

$$k = \frac{m_4}{m_2^2}$$

$$m_r = \frac{1}{N} \sum_i (x_i - \bar{x})^r$$

$$(N-1)^{(3)} = (N-1)(N-2)(N-3)$$

N is the total number of point locations

x_i (i = 1,....N) is the value of the variate at each of N point locations

w_{ij} = 1 if points i and j are neighbours in distance class d, and 0 otherwise

Programmes for calculating *I(d)* and *z(d)* using the above formulae (see Methods) were written and compiled in BASIC by the author.

APPENDIX 4: Formulae for $K(t)$ and $K_{12}(t)$.

The function $K(t)$ is a second order statistic defined as:

$K(t) = \rho^{-1}$ E[number of points within a distance t of a randomly chosen point]

Where ρ is the intensity = the mean number of events per unit area.
The area within a distance t of a randomly chosen point is πt^2, so the expected number of points that lie within this area, assuming a random distribution of points with intensity ρ, is $\rho\pi t^2$. Hence for a random distribution of points

$$K(t) = \pi t^2$$

An unbiased estimator of $K(t)$ is

$$K'(t) = N^{-2} A \sum_{i \neq j} \sum v_{ij}^{-1} H(u_{ij})$$

Where:

A is the plot area

N is the total number of point locations in area A

u_{ij} is the distance between points i and j

$H(u_{ij})$ takes the value 1 if $u_{ij} \leq t$, and 0 otherwise

v_{ij} is defined for a rectangular plot as follows:

Suppose A is the rectangle $(0, a) \times (0, b)$. Let the coordinates of point i be (x_1, x_2). Then let $d_1 = \min(x_1, a - x_1)$ and $d_2 = \min(x_2, b - x_2)$; d_1 and d_2 are the distances from i to the nearest vertical and horizontal edges of A.

To calculate v_{ij} we distinguish two cases:

(1) If $u_{ij}^2 \leq d_1^2 + d_2^2$

$$v_{ij} = 1 - \pi^{-1} \left[\cos^{-1} \left(\frac{\min(d_1, u)}{u} \right) + \cos^{-1} \left(\frac{\min(d_2, u)}{u} \right) \right]$$

(2) If $u_{ij}^2 > d_1^2 + d_2^2$

$$v_{ij} = \frac{3}{4} - (2\pi)^{-1} \left[\cos^{-1} \left(\frac{d_1}{u_{ij}} \right) + \cos^{-1} \left(\frac{d_2}{u_{ij}} \right) \right]$$

These formulae apply to values of u_{ij} in the range $0 \leq u_{ij} \leq \frac{1}{2}\min(a, b)$.

The function *K(t)* can apply to a bivariate point process:

$K_{12}(t) = \rho^{-1}$ E[number of points of species 1 within a distance *t* of a randomly chosen point of species 2]

If the two species are independent (ie., distributed at random with respect to each other) then

$$K_{12}(t) = \pi t^2$$

An estimator of $K_{12}(t)$ is

$$K'_{12}(t) = (N_1 + N_2)^{-1} [N_2 K_{\overline{12}}(t) + N_1 K_{\overline{21}}(t)]$$

Where:

$$K_{\overline{12}}(t) = (N_1 N_2)^{-1} A \sum_{i=1}^{N_1} \sum_{j=1}^{N_2} v_{ij}^{-1} H(u_{ij})$$

$$K_{\overline{21}}(t) = (N_1 N_2)^{-1} A \sum_{i=1}^{N_2} \sum_{j=1}^{N_1} v_{ij}^{-1} H(y_{ij})$$

u_{ij} is the distance from the *i* th species 1 to the *j* th species 2

y_{ij} is the distance from the *i* th species 2 to the *j* th species 1

Programmes for calculating *K(t)* and $K_{12}(t)$ were written and compiled in BASIC by the author.